THE UNIVERSITY OF ALBERTA

ECOLOGY OF PLANKTONIC ROTIFERA IN A SHALLOW

EUTROPHIC LAKE OF WESTERN CANADA

by

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ABSTRACT

The population dynamics of the planktonic rotifers of Hastings Lake, Alberta were studied from May 1975 to July 1976. The major emphasis was on the environmental control of the distribution and abundance of the different species and on the adaptive significance and mechanism of cyclomorphosis in the genus Keratella. Environmental factors studied included temperature, food, oxygen, and predation. Duration of egg development was ascertained for some species.

Hastings Lake is highly eutrophic with dense concentrations of Chlorophyta and Cryptophyta occurring in the spring and fall and massive blooms of Cyanophyta occurring in the summer. Oxygen depletion occurs during warm, calm weather and under the ice. The three dominant rotifers, Keratella quadrata, K. cochlearis, and K. earlinae, were perennial, existing through widely varying environmental conditions. The birth rates of these and other rotifers were significantly affected by temperature. The birth rates of Keratella were also affected by the concentration of "edible" phytoplankton. Other rotifers, such as Brachionus angularis and Filinia longiseta, only occurred during the summer months. They appeared during times of high water temperatures, high oxygen concentrations, and dense Cyanophycean blooms. The importance of filamentous Cyanophyta as a food source for Brachionus angularis is discussed. Species such as Notholca squamula and Conochilus natans appeared restricted to colder water with high concentrations of "edible" cells.

Results are discussed in relation to hypotheses of population regulation. Environmental factors were important in controlling the population growth. No evidence for an intrinsic control was found, although the data do not lend themselves to a thorough analysis.

My results concerning the cyclomorphosis of Keratella are in contrast to much of the published literature on this subject. Spine length of K. cochlearis and K. earlinae showed a positive relationship with temperature and the longest spines were found at temperatures of approximately 20°C. Spine length of K. quadrata showed a negative relationship with temperature. The importance of cyclomorphosis is discussed in terms of predator avoidance. Some of the lorica and spine lengths were significantly correlated with predator density; however, the importance of predation in causing cyclomorphosis remains obscure. The importance of understanding the natural history of each species to explain cyclomorphosis is indicated.

ACKNOWLEDGEMENTS

throughout the study. Special thanks also to Maureen Lamont for her assistance throughout the project and for her patience and optimism.

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INTRODUCTION

The study of rotifers is a poorly developed field in North
America. There is a paucity of information despite the ease of
collection, world wide distribution, and interesting biology of
rotifers.

In North America, Gilbert (1967, 1973) studied the predator-prey
relationship between Asplanchna and Brachionus with emphasis on the
adaptive significance of cyclomorphosis. King (1967, 1972)
concentrated on laboratory and field populations of Euchlanis dilatata
with special interests in the effects of rotifer age on population
growth and the adaptations for seasonal environments. Edmondson
(1960), one of the leading researchers in rotifer ecology, has
studied population dynamics of rotifers in Bare Lake, Alaska, using
the egg ratio method for determining instantaneous birth and death
rates. George and Fernando (1969, 1970) studied seasonal distribution
of rotifers, particularly Keratella, and the vertical migrations
of rotifers in small lakes in southern Ontario.

In contrast to limited data from North America, European
workers have contributed the vast majority of information on rotifers.
The works of Pejler (1957a,b,c; 1961) deserve special attention.
He studied the seasonal and geographical distributions of rotifers
from Sweden and Lapland and compiled extensive notes on each
species' relationships with environmental factors. Pejler (1962)
also studied the cyclomorphosis of Keratella cochlearis. Ruttner-
Kolisko (1974) contributed to the study of rotifers with her work
concerning the taxonomy and general biology of the planktonic

rotifers. Amren (1964a,b,c), working on Spitzbergen Island, utilized Edmondson's methods for determining instantaneous birth rates and developed interesting theories on the intrinsic control of population density and cyclomorphosis based on the theories of Wesenburg-Lund (1930).

Because of this general lack of field data on planktonic rotifers in North America, particularly western North America, one purpose of my study was to describe the seasonal distribution and population growth of planktonic rotifers from Hastings Lake and compare it to the published reports from other areas.

Population regulation has been a major area of study in ecology since the time of Malthus; it has been the focal point of much discussion and has led to literally thousands of ecological studies. In literature dealing with rotifers, discussion of population regulation has been based on two main viewpoints. Edmondson (1965) described the effects of temperature and food on birth rates of rotifers and suggested that populations are controlled by changing conditions in the environment. Amren (1964a,c), using the same methods as Edmondson and measuring the same environmental factors, reported no correlation between population dynamics and the environment. He suggested an intrinsic control of population growth. Therefore, a second purpose of my project was to study the population dynamics of planktonic rotifers in light of these two views.

A third purpose of my study was to examine the cyclomorphosis of the genus Keratella. This is a particularly difficult field when one considers the vast amounts of conflicting data concerning

cyclomorphosis. The idea was to study cyclomorphosis from the view of adaptive significance. Thus, the problem is not so much how rotifers change shape, but why; ie what are the selective pressures that determine the advantage of cyclomorphosis? I believed that such an understanding could only come from a detailed field study, encompassing as many environmental factors as possible.

DESCRIPTION OF STUDY AREA

Hastings Lake is a small lake in central Alberta, situated approximately 40 km E-SE of Edmonton. It is a eutrophic, non-stratifying lake, subject to pronounced blue-green algal blooms during the summer and severe oxygen depletion under the ice. Ice cover usually lasts from early November to late April. Figure 1 presents a map and the geographic location of the lake. Table 1 presents morphometric parameters.

Bedrock in the area is termed the Edmonton Formation, which is a brackish water formation composed of bentonitic sandstones, clays, and coal seams (Bowser et al, 1962). During Wisconsin time, glaciers deposited a till varying from 7.5 to 30 m thick (Bowser et al, 1962). Hastings Lake lies in this glacial till and was probably formed as a kettle lake (Schwartz and Gallup, in press).

Most of the lake is surrounded by podzolic soils termed Cooking Lake Loam. The area to the northwest of the lake consists of solentzic soils termed Ministik Silty Clay Loam (Bowser et al, 1962).
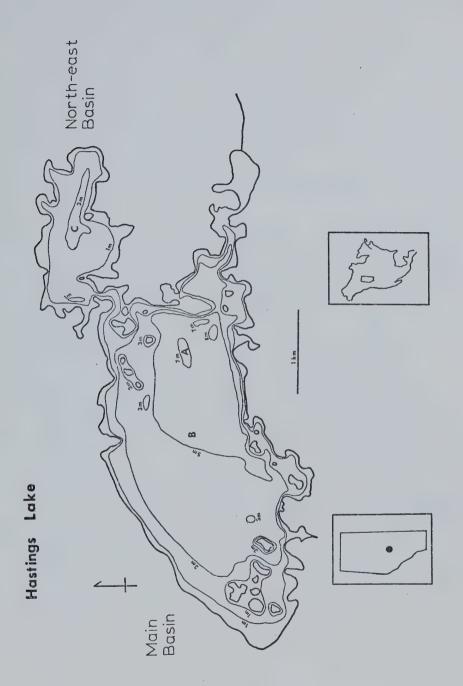
Hastings Lake lies in the North Saskatchewan River drainage basin. In times of high water, Hastings Creek flows from the eastern end of the lake to BeaverHill Lake. During the study there was no perceptible flow in the creek.

Climate of the area is continental with warm summers and cold winters. Air temperature maxima, usually in July, rarely exceed 32°C and winter temperatures rarely drop below -40°C. Annual precipitation averages 40-45 cm, 70 per cent of this falling as rain and the remainder as snow. Most of the rain falls during June, July, and

Figure 1. Outline of Hastings Lake, with depth contours, sampling
stations (A,B,C), and geographical location. Stations A
and B in main basin. Station C in north-east basin.

Hastings Lake

North-east Basin

Main Basin

1 km

TABLE 1

Morphometry of Hastings Lake

	Main Basin		North-east Basin	
Area	7.3	km^2	1.4	km^2
Volume	ca. 0.20	km^3	ca. 0.02	km^3
Maximum Length	5105.0	m	2134.0	m
Effective Length	4953.0	m	2134.0	m
Maximum Width	1859.0	m	991.0	m
Effective Width	1859.0	m	991.0	m
Maximum Depth	8.1	m	3.0	m
Mean Depth	2.7	m	1.5	m
Shoreline Length	20.5	km (without islands)	7.9	km (without islands)
Shoreline Development	2.14		1.86	
Volume Development	1.01		1.52	
Elevation		735.0	m	

August. During the ice-free months the wind normally approaches the lake from the north-west with an average speed of 15 km/h.

Much of the natural vegetation around the lake has been cleared for agricultural purposes, particularly cattle pastures. The remaining natural vegetation is dominated by Populus tremuloides and and Populus balsamifera with scattered patches of Picea glauca.

A few houses and cottages are located around the lake, particularly on the south shore of the main basin. Because of blue-green algal blooms, the lake is used sparingly for summer recreation, but it does attract waterfowl hunters in the fall. According to local residents the lake supported populations of Perca flavescens and Esox lucius until 1970. During my study no evidence of fish was found.

MATERIALS and METHODS

Because of the field nature of this project, most of the methods
discussed below describe the collection, enumeration and measurement
of zooplankton, the calculation of birth rates for certain rotifer
species, and the monitoring of selected environmental factors.
Laboratory experiments, to determine the duration of eggs at specific
temperatures, will be described after the field methods.

GENERAL

The map of Hastings Lake (Fig. 1) shows the location of
sampling stations A, B, and C with depths of 8, 6, and 3 metres
respectively. Routine sampling began on May 23, 1975 and was
terminated on July 2, 1976. Station B was not sampled after
November 2, 1975. During the ice-free period, sampling was carried
out from a 14 foot boat equipped with a 15 horsepower motor. In
winter, a snowmobile was used for transportation. Holes in the ice
were made with a power auger.

ZOOPLANKTON

Zooplankton samples were taken twice a week during spring and
summer 1975. In autumn 1975, sampling frequency was reduced to about
one sampling period every five days. In winter 1975-1976, samples
were taken biweekly with the exception of December 1975 when only
one sampling period was performed due to ice conditions. After
ice break-up on April 27, 1976 the original semiweekly sampling was
resumed.

Samples were taken from each station at 1 metre intervals throughout the water column. During winter, the ice surface was considered the surface of the water. A Schindler-modified Patalas plankton trap of 9 liters (Schindler, 1969), constructed of transparent plexiglass and fitted with a #25 (64µ), "Nitex", plankton net, was used to collect zooplankton. Samples were placed in four ounce glass bottles and preserved in the field with 5% formalin. In the laboratory each sample was diluted to 75 ml in a flask, mixed by shaking, and subsampled with a 2 ml Henson-Stempel pipet. The subsample was poured into a counting chamber and allowed to settle. All rotifers and cladocerans were identified to species and the copepods were identified to genus. However copepod nauplii stages were not identified as cyclopoid or calanoid. Samples were counted on a Wild M40 inverted microscope at 40X. For each zooplankton species the population density at each station was computed by averaging numbers recorded at each depth. Station egg ratios, for egg carrying rotifer species, were computed by dividing the station total number of eggs by the station total number of females.

The ratio of eggs per female was used to determine instaneous birth rates according to equation (1) from Paloheimo (1974),

$$b = \frac{\ln \left(\frac{Ct}{Nt} + 1 \right)}{D}$$

where   b   = instantaneous rate of birth

             C_t = number/liter of eggs at time t

             N_t = number/liter of amictic females at time t

             D   = duration of development of eggs

Since some illoricate rotifers were difficult to identify to species when preserved, living rotifers were collected with a #25 Wisconsin-type plankton net and returned to laboratory. Live specimens were mounted in a drop of lake water and observed through a Wild M20 microscope. For certain species it was necessary to remove the mastax from the rotifer's body to ensure proper identification. This was done by mounting a rotifer in a dilute solution of Chlorox, which dissolved the soft tissues but left the mastax intact (Edmondson, 1959). Rotifers were identified using keys from Edmondson (1959), Chengalath et al. (1971), and Ruttner-Kolisko (1974). Crustaceans were identified using keys from Brooks (1959), Wilson and Yeatman (1959), Pennak (1963), and Brandlova et al. (1972).

To investigate temporal variation of certain species, measurements were made of body and spine lengths. Measurements were made on samples from stations A and C, which were collected biweekly during the ice-free periods and monthly during the winter. Animals were mounted in glycerin and measured at 400X on a Wild M20 equipped with a calibrated ocular micrometer. Two measurements were made on specimens of Keratella cochlearis and K. earlinae, ie lorica length (from base of median anterior spines to base of posterior spine) and posterior spine length. Keratella quadrata was measured for lorica length (from base of median anterior spines to median

posterior edge of lorica) and length of left and right posterior spines. The lengths of the two spines were subsequently averaged.

PHYTOPLANKTON

Phytoplankton samples were collected biweekly during ice-free periods and monthly during winter. Samples were taken from station A at the surface and at 2, 4, and 6 metres and from station C at the surface and at 2 metres. A 1200 ml brass Kemmerer water bottle was used to collect the samples which were preserved in the field with Lugol's solution and stored in 25 ml vials.

Samples were identified to genus according to Prescott (1970) and counted on a Wild M40 inverted microscope according to the method described in Lund et al (1958). Only those cells that I considered edible by the rotifers were counted but relative abundances of Cyanophyta were noted.

BACTERIA

Sampling the planktonic bacteria populations began on May 28, 1975. On this date and on June 23, 1975 samples were taken from station A at the surface and at depths of 3 and 7 metres. From July 7, 1975 until completion of the project samples were taken at the same times and locations as the phytoplankton samples. Samples were collected with a 1200 ml brass Kemmerer water bottle, placed in sterilized glass bottles, and returned within twenty-four hours to the Provincial Laboratory of Public Health for analysis. Bacteria cells were enumerated by the standard plate count method at 35°C. Samples were diluted when the counts were in excess of

3,000 cells per ml.

PARTICLE ENUMERATION AND SIZE ANALYSIS

During ice-free periods water samples for particle size analysis
were taken biweekly from station A at the surface and at depths of
2, 4, and 6 metres and from station C at the surface and at 2 metres.
During winter, samples were collected monthly from the same sites.
Samples were collected with a 1200 ml brass Kemmerer water bottle,
placed in clean 4 oz glass jars, and fixed in the field with 2%,
0.45 μ filtered, buffered formalin. Until December 1975 samples
were analyzed with a Model B Coulter Counter (Coulter Electronics,
Inc., Hialeah, Florida). Samples collected from December 1975 until
completion of the project were analyzed with a Model TA II Coulter
Counter. Samples were prepared for analysis by mixing 22.5 ml lake
water with 2.5 ml 0.45 μ filtered 5.0% NaCl and 75 ml 0.45 μ
filtered 0.5% NaCl. Both counters determine the number and volume
of particles within discrete diameter ranges.

WATER CHEMISTRY

Water samples for chemical analysis were collected from stations
A and C at 1 metre intervals. Samples were collected biweekly
during 1975, then monthly at station A and bimonthly at station C
in 1976. Samples were taken with a two liter polyethylene Van Dorn
water sampler, placed in screw-top polyethylene bottles, returned to
the laboratory, filtered and frozen until analysis. Water was analyzed
for pH, conductivity, chlorine, total and calcium hardness, total
and phenolphthalein alkalinity, total phosphate and orthophoshate,

total Kjeldahl nitrogen, organic nitrogen, and nitrate nitrogen.
Samples were analyzed by Mrs. G. Hutchinson in the Department of
Zoology water laboratory according to A.P.H.A.'s Standard Methods
(1971).

TEMPERATURE

Temperature recordings were taken with a Model 54 Dissolved
Oxygen Metre (Y.S.I. Co., Yellow Springs, Ohio) until December
1975. During 1976 a Dissolved Oxygen Metre TDO-2 (Hydrolab Corp.
Austin, Texas) was used. Temperature readings were taken on all
sampling dates from each station at 1 metre intervals.

DISSOLVED OXYGEN

Dissolved oxygen readings were taken with the same instruments
and at the same stations and depths as were the temperature readings
from June 23, 1975 until completion of the sampling period. The
readings in ppm were converted to percent saturation using Mortimer's
nomogram (1956).

EGG DURATIONS

Laboratory experiments were neccessary to determine duration of
development of eggs, D in equation (1). Rotifers were collected
from Hastings Lake with a Wisconsin Plankton net and returned live
to the laboratory. Non-ovigerous females were isolated from samples
and placed in small chambers suspended in large bowls of lake
water as in Amren (1964). The water was maintained at a known,
constant temperature ($\pm$ 0.5 C^{o}). The chambers were plastic vials

with holes cut in the sides; 64μ netting secured over the holes
kept the rotifers in the chambers but allowed water and food to flow
through. Animals were checked hourly and when an ovigerous animal
was found it was isolated in another chamber. By checking individual
ovigerous animals at hourly intervals it was possible to determine
when eggs were hatched. Approximate laying and hatching times gave
an estimate of duration of development at experimental temperatures.
A least squares regression line was fitted to the data points for
each species and values used in equation (1) were read from this line.

THE PHYSICAL-CHEMICAL ENVIRONMENT

WEATHER DURING STUDY

Precipitation and air temperature data from Environment
Canada, Atmospheric Environment, recorded at the Edmonton Inter-
national Airport, 45 km W-SW of Hastings Lake, are presented in
Figure 2. During June and July 1975 monthly mean temperatures were
close to normal for the area. August however, was a few degrees
cooler and September a few degrees warmer than average. From
November 1975 to May 1976 each monthly mean was higher than the
average temperature, especially in January and February, when
temperatures were a full 4 C^o higher than usual. April was also a
warm month, with maximum temperatures over 20°C during the first and
second week. June 1976, in contrast to the mild winter and spring
was slightly cooler than average. The precipitation graph followed
the usual pattern with yearly maxima in June, July, and August.
Snowfall was close to average during winter months with the exception
of April 1976 when only 4.8 cm fell compared to the usual 13.7 cm.

TEMPERATURE

Because of its shallow depth and susceptibility to wind,
Hastings Lake did not form a true hypolimnion. Thus isotherms
recorded during ice-free periods can be explained as a result of air
temperatures and strength and duration of wind. Under the ice the
lake exhibited inverse thermal stratification. Heating of the lower
depths during winter was probably a combination of heat transfer
from sediments and influx of dense, warm water from the solar
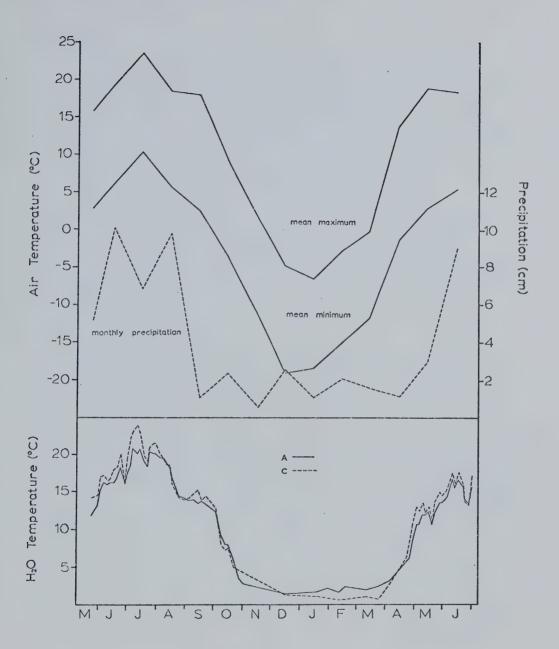
Figure 2. Maximum and minimum air temperatures, and total monthly
precipitation; Edmonton International Airport.
Mean water temperature at stations A and C.
1975-1976.
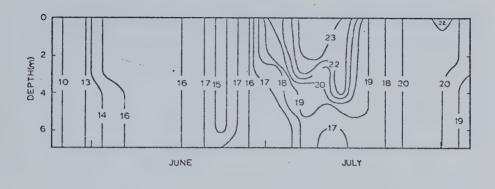
heated littoral zone (Wetzel, 1975).
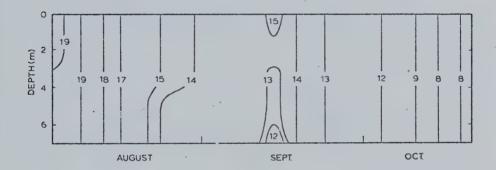
Main Basin

According to local residents, spring break-up of 1975 occurred in early May. Water temperatures rose rapidly in late May, early June, and were equal to the air temperatures in late June (Fig. 3). The lake was homoiothermal during spring 1975. During early July the main basin exhibited a thermal gradient with the greatest temperature difference being 6 C^o between the surface and lake bottom. On July 18 a rainstorm accompanied by high winds destroyed the gradient and left the lake homoiothermal at 19^oC. The lake remained at $18-20^oC$ for two weeks after the storm but never regained the thermal gradient.

The fall cooling trend began in early August and continued slowly until freeze-up on November 6. The lake was homoiothermal with the exception of a few days in mid September when the weather was calm and warm. Under the ice, water temperatures were inversely stratified; approximately 1^oC near the ice and 3^oC at the lake bottom. This temperature regime was stable for most of the ice-covered period. Warming of the water during spring 1976 began under the ice. Ice break-up in the main basin occurred on April 26; approximately two weeks earlier than usual according to local residents. Immediatly after ice break-up the water warmed rapidly; during May temperatures continued to increase but at a slower rate. Water temperatures in June 1976 were slightly colder than those of June 1975.
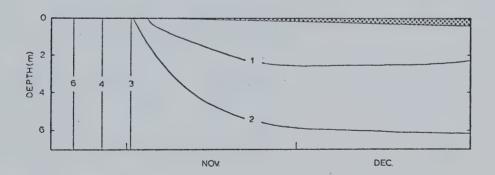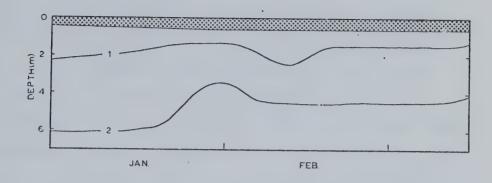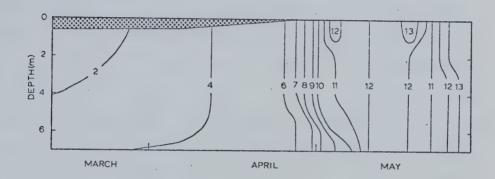
Figure 3. Isotherms (°C) at station A, 1975-1976. Stippled areas represent ice drawn to scale. Continued.
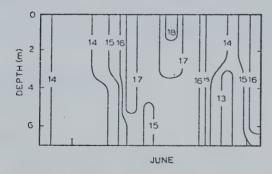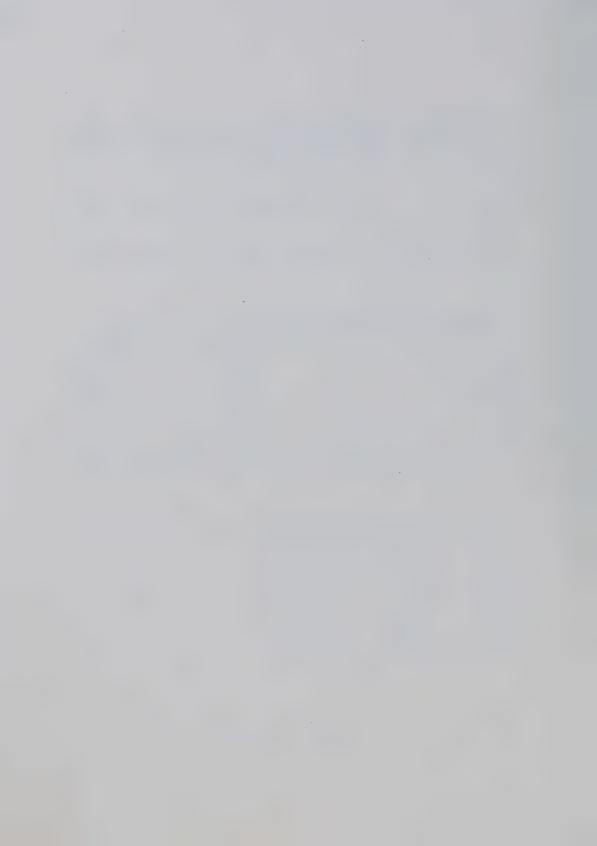
Figure 3. Continued.

North-east Basin

Because of the relative shallowness of station C, the thermal regime differed from that at station A in three ways: average temperatures were more extreme at station C, ie warmer in summer and colder in winter; changes in temperature occurred faster at station C; and the summer thermal gradient at station C was transitory and poorly developed. The 1975 spring and early summer isotherms at station C (Fig. 4) show the same homoiothermal pattern as station A but at a higher average temperature, with greater day to day fluctuations (Fig. 2). The water temperatures in early July showed a slight gradient. Water temperature dropped following the storm of July 18 but rose to over 20°C between July 25 and August 4. After August 4 the average temperature dropped slowly until freeze-up around November 4, 1975. Under the ice, temperatures averaged 1°C and showed an inverse stratification. After ice break-up, approximately April 21, 1976, the lake warmed rapidly to 13°C on May 4. During May and June the lake was homoiothermal and temperatures varied according to air temperature fluctuations.

DISSOLVED OXYGEN

Main Basin

Oxygen isopleths for late June showed high, uniform oxygen saturations (Fig. 5). Distinct oxygen stratification occurred during early July with 170% saturation at metre 2 and 10% saturation at metre 7. The high oxygen concentrations near the surface were indicative of rapid phytoplankton production.
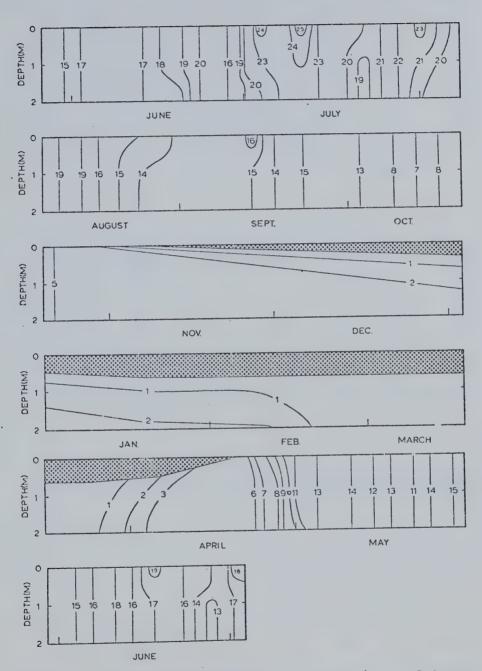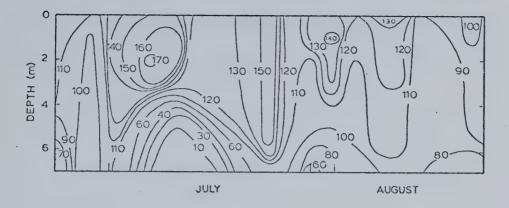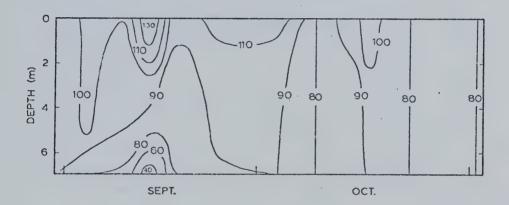
Figure 4. Isotherms (°C) at station C, 1975-1976. Stippled areas represent ice drawn to scale.
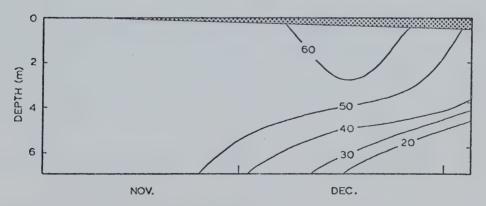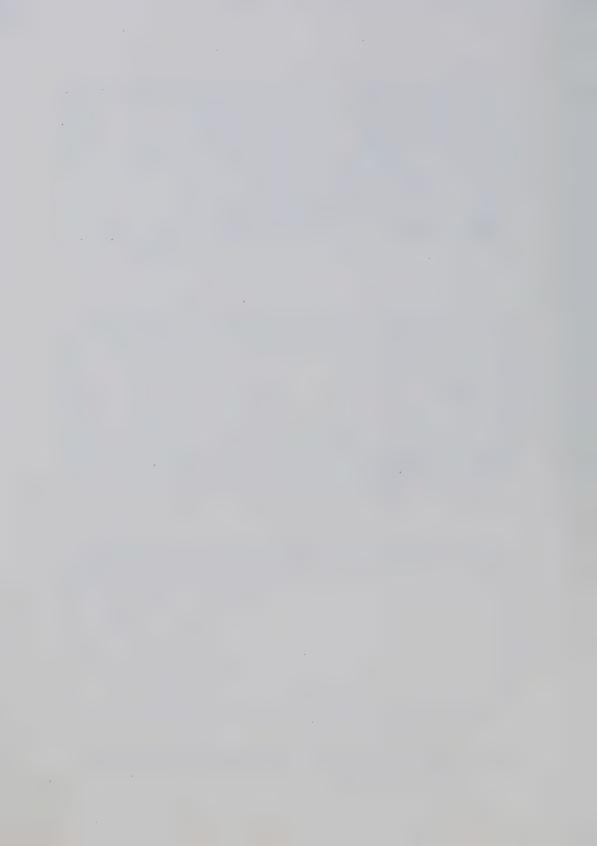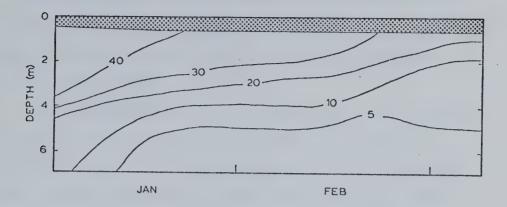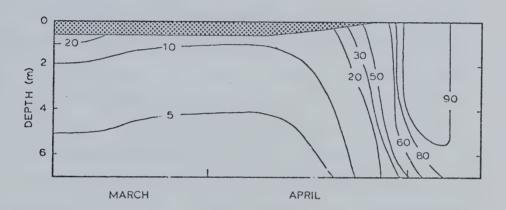
Figure 5. Isopleths of percentage oxygen saturation at station A, 1975-1976. Stippled areas represent ice drawn to scale. Continued.
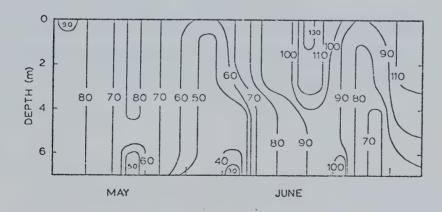
Figure 5. Continued.

After the storm of July 18, the stratification disappeared but the saturation remained above 100% until mid-August. The oxygen stratification period lasted longer after the storm than did the thermal stratification.

From mid-August until freeze-up, oxygen concentrations remained stable, fluctuating between 80 and 100% saturation. One brief exception to this occurred in mid-September when calm, warm weather prevailed; the surface oxygen concentration rose to 130% saturation while the bottom declined to 40% saturation.

By mid-December 1975 oxygen concentrations had dropped to 60% saturation at the ice and 20% saturation at the sediments. Oxygen saturation continued to drop until a mimimum was reached on April 6, 1976, with 10% saturation near the ice and less than 5% below the 5 metre depth. Phytoplankton production under the ice probably caused the increased saturation levels in late April.

Oxygen saturation increased rapidly after break-up and was approximately 90% on May 7, 1976. The remainder of May was stable with oxygen saturations averaging 70%.
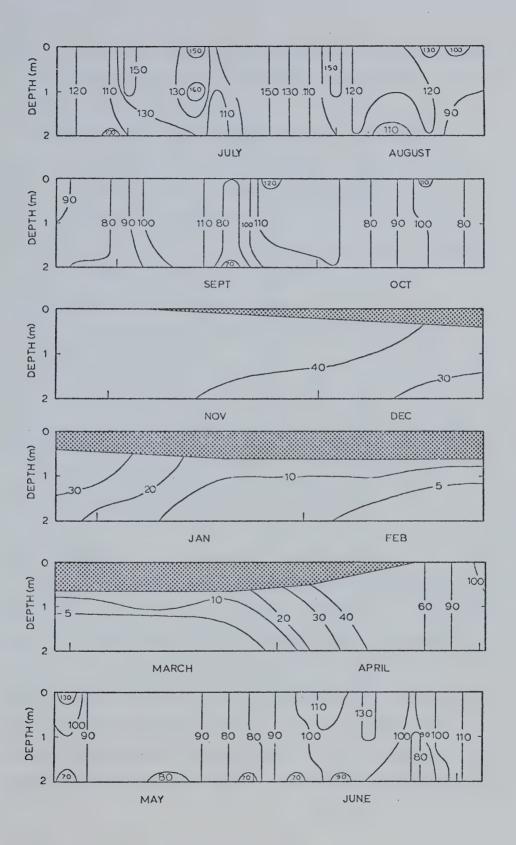
During overcast weather in early June, the oxygen saturation declined with water at most depths less than 50% saturated. By mid June the weather had cleared and the oxygen saturation increased to 80%.
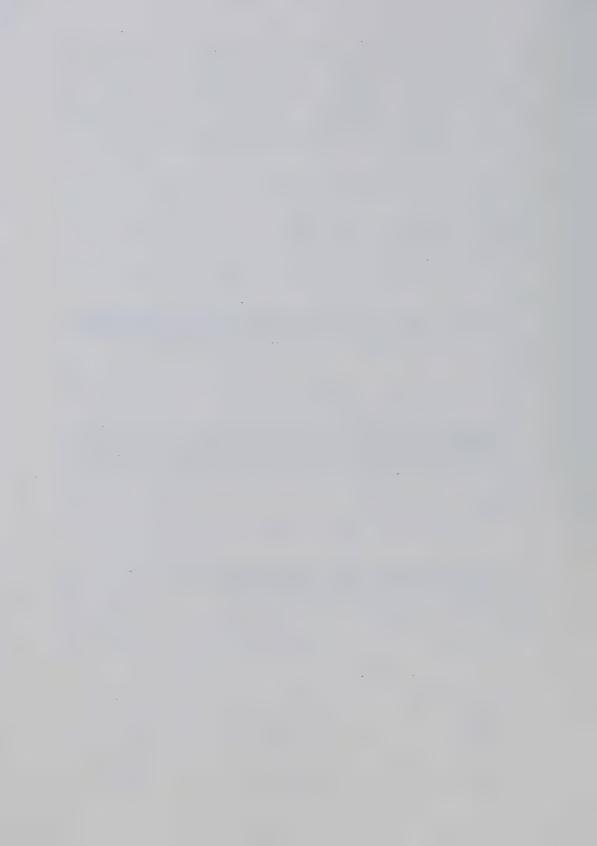
North-east Basin

Oxygen saturations were high at station C during June 1975 (Fig. 6). During early July, the saturation rose to 160% but no oxygen depletion near the sediments was noted as in the main basin.

Figure 6. Isopleths of percentage oxygen saturation at station
C, 1975-1976. Stippled areas represent ice drawn to
scale.

Late July and August also showed high oxygen saturation, an indication of high primary productivity. During October the saturation dropped slightly but was stable at 80%.

Under the ice the oxygen saturation dropped more quickly at station C than at station A. By mid December the oxygen saturation was 40% and by late January the saturation had dropped to 10%. Low levels of oxygen were maintained until early April when increasing phytoplankton productivity raised the saturation to 30%. The spring increase in oxygen began earlier at station C than did the corresponding increase in the main basin.

After spring break-up the saturation rose rapidly and was approximately 100% by early May. During the rest of May and the first half of June, the saturation was stable, fluctuating between 80% and 90%. With the advent of clear weather in mid-June, the oxygen saturation rose to over 100% and, with the exception of 80% values in late June, remained over 100% until July 2. The 80% values in late June were associated with cold rainy weather.

WATER CHEMISTRY

Results of the water chemistry analyses are shown in Tables 2 and 3. The pH in Hastings Lake was always alkaline, the lowest value being 7.8 recorded from station A in February 1976. No obvious seasonal trend was noted and values at stations A and C were similar. Conductivity values varied considerably but a distinct increase was noted during the winter. Values at stations A and C often differed considerably on any particular day but neither station showed a continuously higher reading. Total hardness values show

TABLE 2

Chemical parameters at station A.
All units are in mg/l except pH and conductivity (μmhos/cm).

	pH	Hardness CaCO$_3$ Calc.	Total	Cond.	Cl$^-$	SO$_4$	Alkal. as CaCO$_3$ Phenol.	Total
21/05/75	8.5	98	279	724	7.6	263	8	197
06/06/75	9.2	42	189	586	7.7	157	20	134
19/06/75	8.8	105	294	885	11.4	281	12	198
03/07/75	9.2	100	286	818	10.3	296	30	203
18/07/75	9.1	50	208	615	7.3	214	16	142
07/08/75	9.1	44	215	584	9.2	215	19	151
20/08/75	8.8	45	235	705	11.2	232	12	165
06/09/75	9.2	49	214	632	9.3	193	24	157
20/09/75	9.0	46	215	574	8.6	192	22	150
04/10/75	9.2	90	285	820	14.9	233	32	201
25/10/75	8.9	100	295	691	12.0	234	24	217
03/12/75	8.5	100	320	917	10.9	288	8	222
13/01/76	9.0	88	302	765	10.6	184	26	213
19/02/76	7.9	77	290	1075	12.7	279	--	--
16/03/76	8.6	123	344	983	11.3	204	17	272
06/04/76	8.8	73	346	1087	8.8	284	--	--
26/04/76	8.0	76	291	945	7.2	300	--	253
27/05/76	8.4	86	303	947	7.2	244	--	--
23/06/76	8.3	88	287	999	7.0	240	--	--

TABLE 2 (continued)

All Phosphate readings expressed as PO_4.

	Ttl PO_4	Ortho PO_4	Orgn PO_4	Ttl Kjl N	Orgn N	NO_3-N
21/05/75	0.31	0.06	0.14	2.15	2.13	0.07
06/06/75	0.28	0.08	0.12	1.75	1.57	0.05
19/06/75	0.49	0.34	0.10	2.49	2.43	0.07
03/07/75	0.43	0.29	0.11	2.19	2.07	0.06
18/07/75	0.50	0.25	0.10	1.92	1.91	0.03
07/08/75	0.36	0.11	0.19	2.28	2.17	0.09
20/08/75	0.39	0.08	0.14	2.38	2.10	0.05
06/09/75	0.26	0.04	0.14	2.22	2.14	0.07
20/09/75	0.29	0.08	0.10	2.16	2.09	0.04
04/10/75	0.32	0.06	0.13	2.31	2.22	0.06
25/10/75	0.38	0.04	0.16	2.25	2.19	0.06
03/12/75	0.25	0.05	0.12	2.63	2.44	0.13
13/01/76	0.87	0.55	0.14	3.30	2.96	0.09
19/02/76	0.97	0.76	0.12	--	--	--
16/03/76	1.13	0.72	0.20	3.36	2.96	0.16
06/04/76	0.86	0.56	0.18	2.62	2.23	0.13
26/04/76	0.73	0.40	0.25	--	--	--
27/05/76	0.64	0.37	0.13	--	--	--
23/06/76	0.69	0.48	0.09	--	--	--
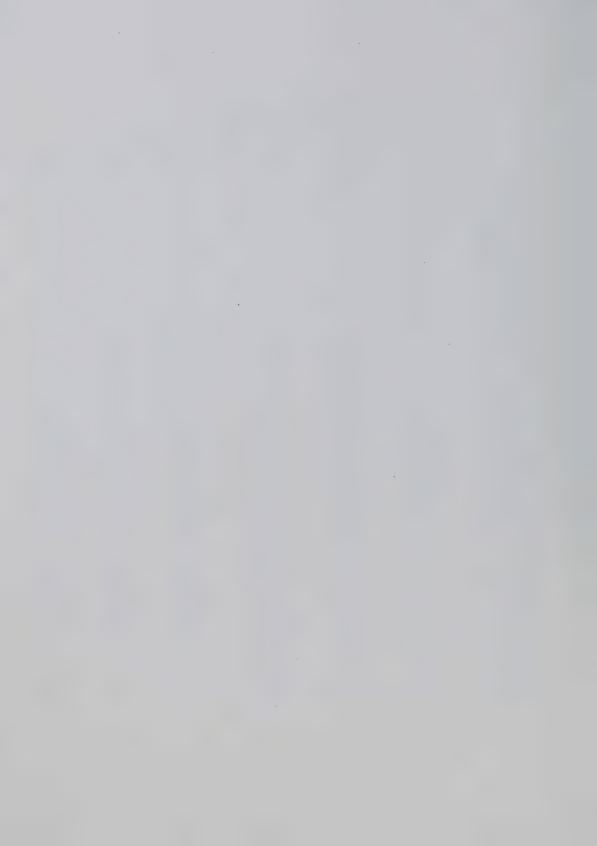
TABLE 3

Chemical parameters at station C.
All units are in mg/l except pH and conductivity (μmhos/cm).

	pH	Hardness CaCO$_3$ Calc.	Total	Cond.	Cl$^-$	SO$_4$	Alkal. as CaCO$_3$ Phenol.	Total
03/06/75	9.2	91	271	726	9.0	267	28	177
19/06/75	8.8	75	252	743	7.9	162	14	163
02/07/75	9.1	45	223	597	9.4	191	18	140
17/07/75	9.1	46	198	578	7.6	172	18	138
07/08/75	9.1	40	218	673	10.6	205	24	149
20/08/75	9.0	44	216	737	10.4	202	17	152
06/09/75	8.8	55	201	745	8.2	181	17	159
20/09/75	9.2	56	228	671	10.2	233	25	164
25/10/75	8.7	106	283	898	10.0	229	18	212
11/06/76	8.5	111	300	714	9.3	186	8	226
02/07/76	8.8	113	288	698	12.4	177	22	226
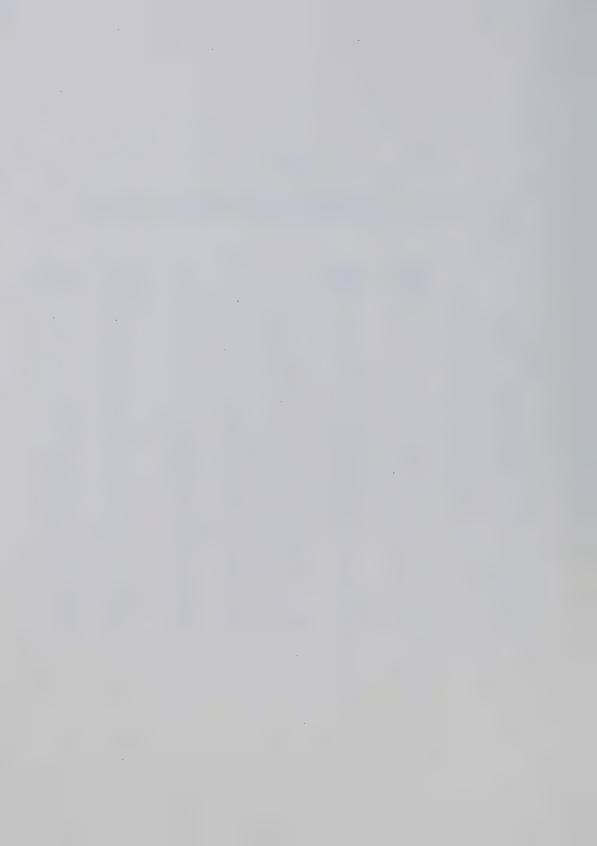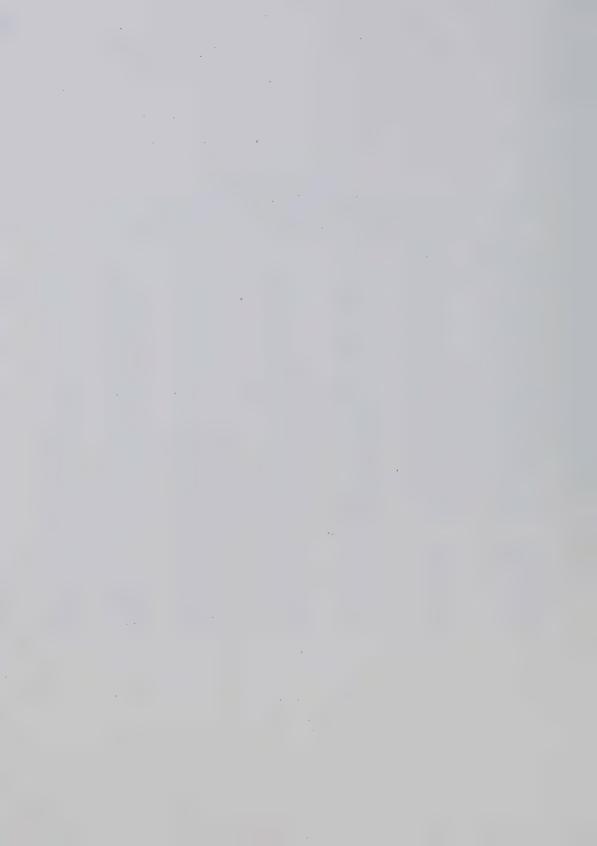
TABLE 3 (continued)

All Phosphate readings expressed as PO_4.

	Ttl PO_4	Ortho PO_4	Orgn PO_4	Ttl Kjl N	Orgn N	NO_3-N
05/06/75	0.42	0.19	0.12	2.04	1.96	0.04
19/06/75	0.65	0.37	0.16	2.38	2.15	0.07
02/07/75	0.43	0.21	0.13	2.39	1.87	0.04
17/07/75	0.86	0.32	0.33	2.26	2.24	0.04
07/08/75	0.36	0.12	0.10	2.51	2.38	0.07
20/08/75	0.37	0.05	0.10	2.51	2.40	0.07
06/09/75	0.33	0.04	0.11	2.06	1.89	0.05
20/09/75	0.23	0.02	0.12	2.29	2.20	0.04
04/10/75	0.33	0.07	0.20	2.07	2.00	0.05
25/10/75	0.40	0.04	0.22	3.05	2.99	0.13
06/04/76	0.44	0.18	0.16	3.20	--	0.04
11/06/76	0.56	0.25	0.17	2.52	2.52	0.05
02/07/76	0.53	0.22	0.18	2.55	2.55	0.08

Hastings Lake to be a hardwater lake. Both calcium and total hardness were lowest during summer and early fall. Low values were also recorded in early June 1975 at station A. At both stations A and C, total alkalinity was high in the winter months but phenolphthalein alkalinity showed no obvious trends. Chloride readings show the lowest values during spring and early summer at station A. Lack of sufficient data makes it impossible to determine whether the same pattern held at station C.

Both total phosphate and orthophosphate showed high concentrations in late winter at station A. Readings from spring and early summer 1976 were higher than corresponding readings in 1975. Total and orthophosphate values for station C were usually higher than those at station A. A distinct pulse in both values was noted during July and August 1975.

Total Kjeldahl nitrogen readings were similar at both stations. No seasonal trend was noticed, but the spring and early summer 1975 values appeared low compared to the rest of the sampling period. Organic nitrogen generally followed the pattern of Kjeldahl nitrogen and made up the major portion of each total Kjeldahl reading. Nitrate readings were very low; maxima were found in late fall and through the winter. The high phosphate readings indicate the obvious eutrophic nature of Hastings Lake but, according to Vollenweider (1968), low nitrate levels are indicative of low trophic status. Ruttner (1963), however, has noted that "markedly eutrophic" lakes often show low concentrations of nitrate due to rapid uptake by phytoplankton.

FOOD

Data on food can be broken down into three areas: bacteria populations, phytoplankton populations, and particle size classification and enumeration. In some respects information on particles overlaps the other two areas.

BACTERIA

Because of the inefficiency of plate counts in determining the absolute number of bacteria cells in a water sample (Collins and Kipling, 1957), it is only possible to use the bacteria data in a comparative way. Edmondson (1965) used a factor of 200 to convert plate counts to actual numbers of cells present but admitted the ratio between direct counts and plate counts varied considerably. Since the counts in my study were not converted to biomass as Edmondson's were, the original plate counts were used.

Bacteria population dynamics at stations A and C are illustrated in Figure 7. The population at station A increased steadily during spring and early summer to a maximum in late July and early August. Numbers declined quickly after early August, were very low by October 3, and remained low through fall and into winter with some minor increases. A sudden increase in density was recorded in early April but the population appeared to die out by spring break-up three weeks later. The concentration remained low during May but a strong increase was seen during June, approximately the same time as the 1975 increase. The population at station C showed the same general trends as that at station A but the maxima were higher than
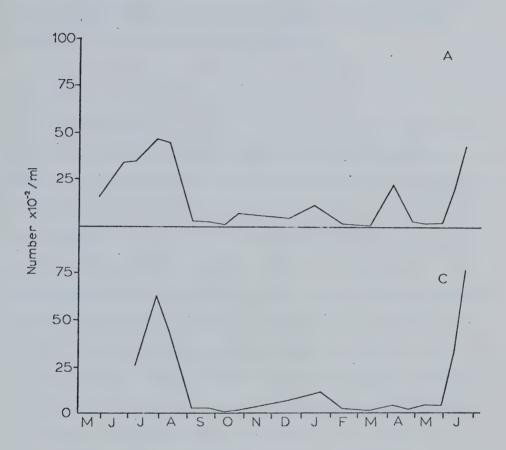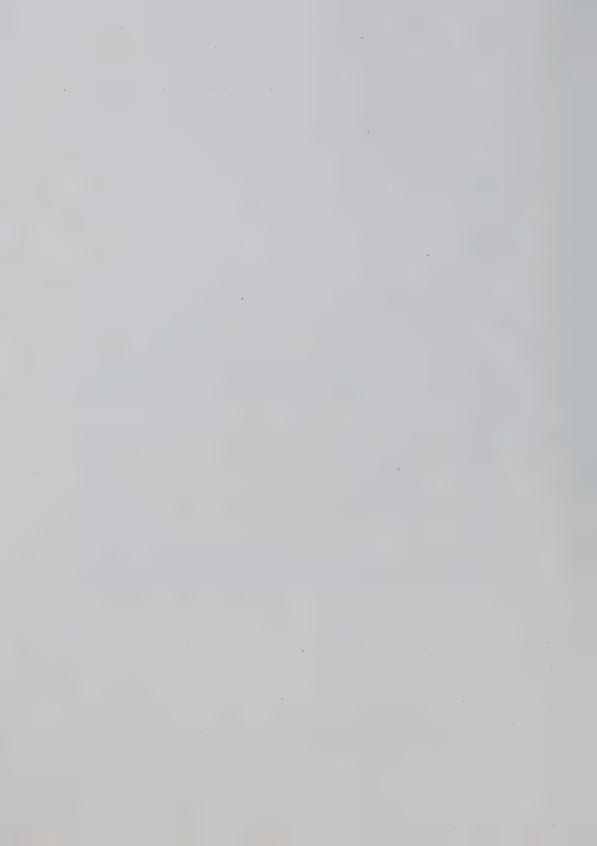
Figure 7. Bacteria cell numbers at stations A and C, 1975-1976.

those at station A.

For most of the year the vertical distribution pattern was
uniform at both stations A and C. During times of high density,
however, bacteria were more numerous at the surface at station A
but more numerous near the bottom at station C. Under the ice
bacteria concentrated near the water surface.

PHYTOPLANKTON

Quantitative data on phytoplankton exist only for those cells
that I considered edible by rotifers. The decision concerning
edibility of cells was based on Pourriot's (1957) work on food habits of
rotifers and on results of Edmondson (1960, 1965). Only small cells
were considered edible, ie cells with both length and width greater
than 15µ were considered inedible. With the exception of
Ankistrodesmus all cells considered edible were essentially spherical
or elliptical in shape. Cells with long spines or processes were
considered inedible. Cells considered edible were free of thick
gelatinous sheaths. Only individual cells were considered edible,
large colonies of otherwise edible cells were considered inedible.
Of the eight cell types selected for counting, four were among
those considered edible by Edmondson (1965). Edmondson did not
count Kirchneriella as he considered it to be colonial. In my
study the cells usually appeared as individuals and were counted.
Relative abundances were recorded for three types of blue-green
algae, since an observation, which will be discussed later, showed
they may have some food value.

Cryptomonas

Cryptomonas, the largest cell included in counts, measured
15-20 µ by 5-10 µ. It may be too large for most rotifer species
to ingest but it has been suggested (Edmondson, 1965) that it may
be important for rotifers such as Polyarthra that possess a virgate
mastax.

Cryptomonas reached maximum numbers in spring and fall (Fig. 8)
and were rare or absent during July and August. At stations A and C
the density of Cryptomonas dropped sharply during late May and early
June 1975, then began a period of slower decline, reaching a minimum
in August. In fall, numbers at both stations increased slowly with
numbers at station C being approximately four times higher than those
at station A; the winter population at station C was ofter an order
of magnitude larger than that at station A. In February, a distinct
increase, which continued until ice break-up, was observed at both
stations. Numbers declined sharply after break-up, then rose and
declined again during June 1976.

During the year Cryptomonas showed a uniform vertical distribution
with the exception of winter months when cells were concentrated
near the ice.

Rhodomonas

Rhodomonas appeared to be a highly "edible" cell. Cell size
averaged 4 µ by 9 µ during summer and slightly longer in winter.
Like Cryptomonas, Rhodomonas appeared in largest numbers during spring
and fall with minima in summer and mid-winter (Fig. 9).
During spring and summer 1975, numbers of Rhodomonas at stations
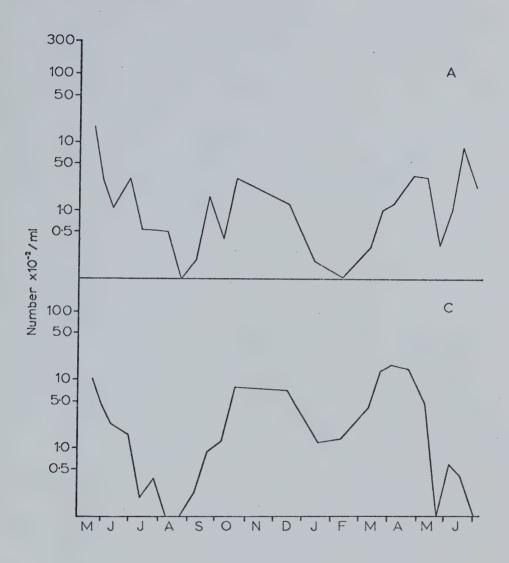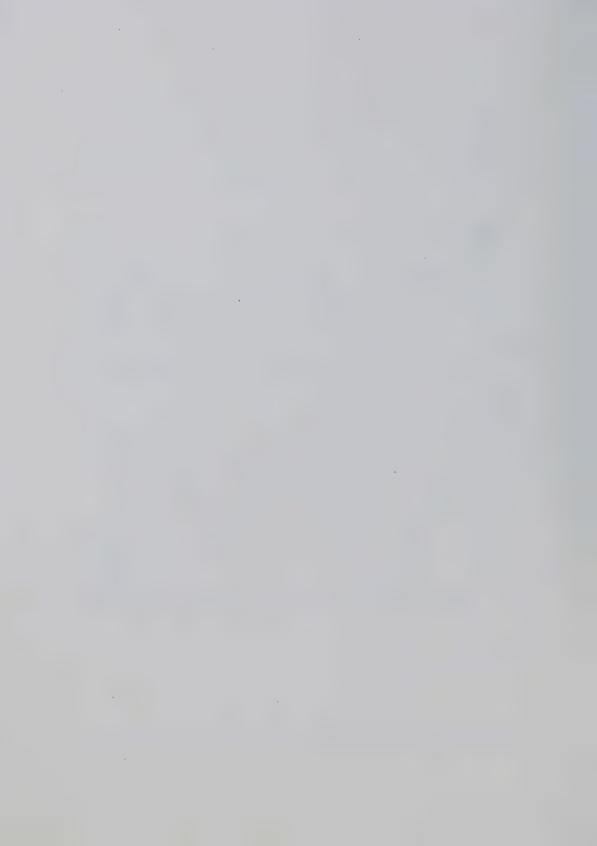
Figure 8. _Cryptomonas_ cell numbers at stations A and C, 1975-1976.
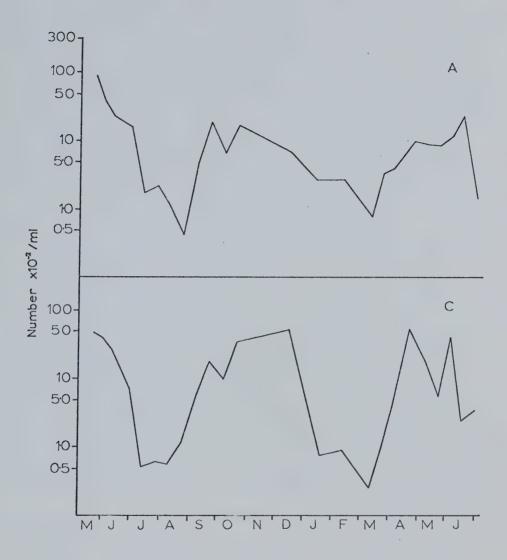
Figure 9. _Rhodomonas_ cell numbers at stations A and C, 1975-1976.

A and C were similar. Densities at both stations declined steadily from late May to August. The fall increase ended with station C being more densely populated in December than station A. The remainder of winter was a period of dramatic decline in numbers at station C and more gradual decline at station A. Numbers at station A increased gradually during spring 1976 while the density at station C increased more rapidly but with a major drop in late May. Both populations appeared to be declining during early summer. While the 1975 and 1976 spring populations were similar at station C, the 1976 spring population at station A was much lower than that of 1975.

Rhodomonas often showed a preference for surface waters (Fig. 10). A strong surface concentration was observed during warm, calm weather in mid-July 1975. Surface concentrations were also noted during winter 1976, probably indicating a preference for higher light levels near the ice. During early spring 1976, vertical distribution was uniform but a preference for the surface was seen again during late May and June. Despite average winds during this time, Hastings Lake showed a gradient in oxygen concentration (Fig. 5), indicating a certain degree of stratification.

Chlamydomonas

A number of species of Chlamydomonas were probably present in Hastings Lake during the study period, ranging from 5μ to 15μ in diameter.

Like Cryptomonas, Chlamydomonas showed a rapid decline in density during early spring 1975, numbers of cells were approximately equal at stations A and C during this time (Fig. 11). Unlike Cryptomonas and
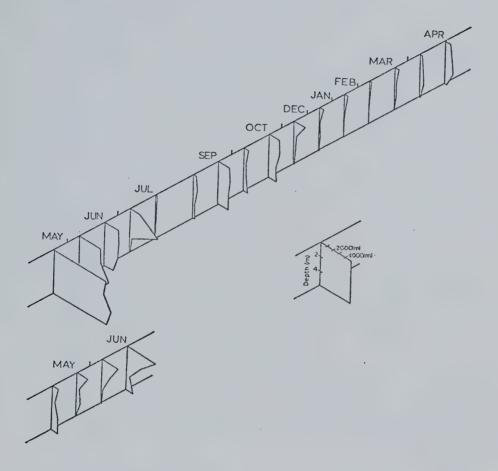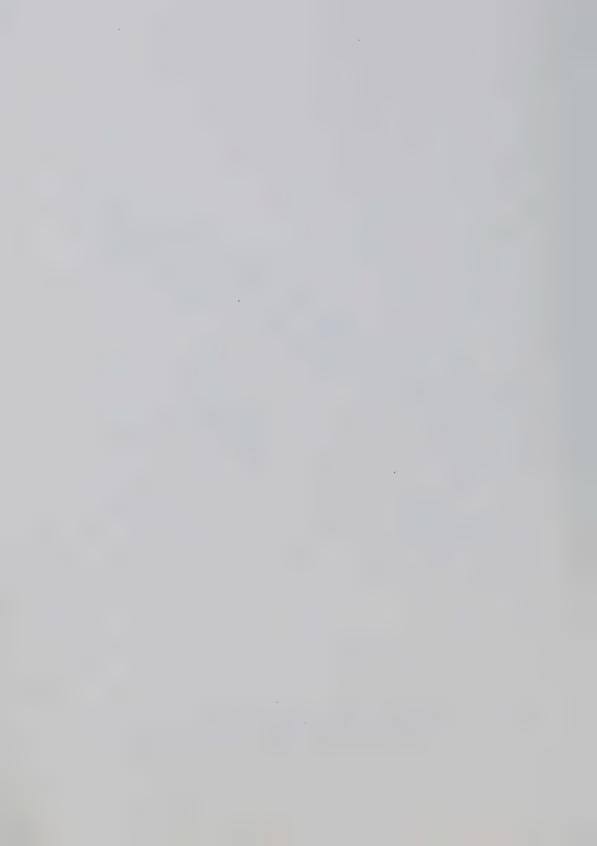
Figure 10. Vertical distribution of _Rhodomonas_ at station A. May 23-July 14, 1975; September 10, 1975-June 18, 1976.
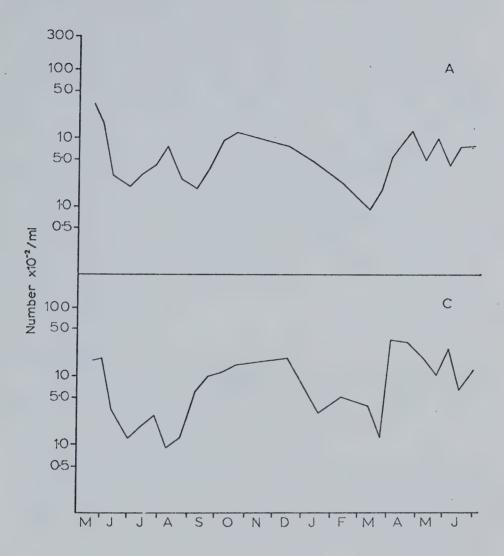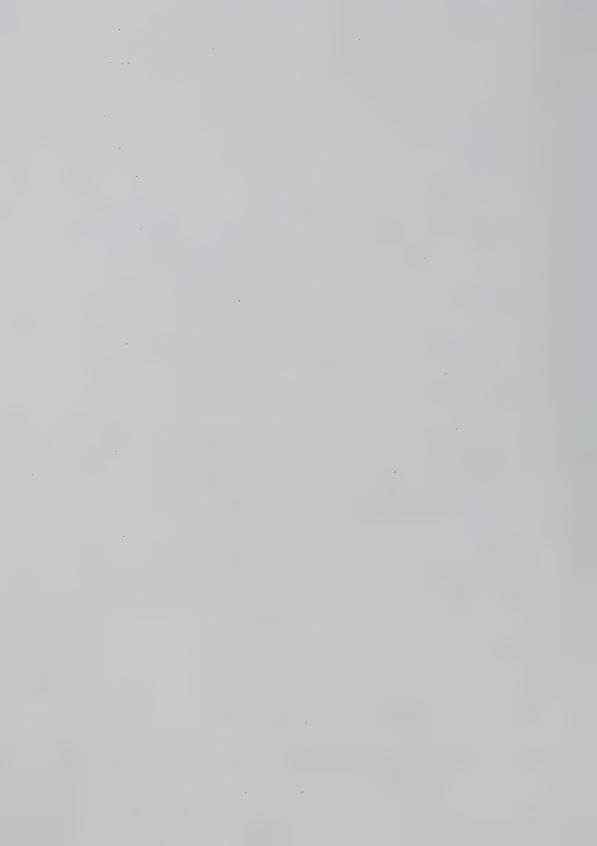
Figure 11. <u>Chlamydomonas</u> cell numbers at stations A and C, 1975-1976.

Rhodomonas, Chlamydomonas showed a distinct increase in numbers at stations A and C during July and August. It is possible that this increase indicated the presence of a species different from the spring population. Following the summer peak, the numbers declined in August but the population increased again during autumn. During winter, numbers at both stations declined to a minimum in March 1976. A sharp increase in numbers occurred in April with higher densities recorded at station C. Both populations appeared to stabilize during May and June. For most of the year, Chlamydomonas showed a uniform vertical distribution (Fig. 12). Surface concentrations were noted during winter and late spring 1976, a situation similar to that of Rhodomonas.

Kirchneriella

As mentioned earlier, Kirchneriella cells are often grouped into colonies and covered by mucilage. The individual cells are crescent-shaped and 5 to 7 μ across the apices.

Populations of Kirchneriella at stations A and C declined sharply during early June, 1975 (Fig. 13). Numbers at the two stations were similar at this time. During the summer months Kirchneriella were rare or absent at both stations. A strong fall pulse occurred in September, 1975 with numbers increasing rapidly but levelling off during October. At station A, Kirchneriella remained at high numbers until March, 1976, while the station C population declined sharply during early winter. In late March and early April 1976 densities were equal at the two stations. In spring 1976 numbers at station A decreased but increased at station C.
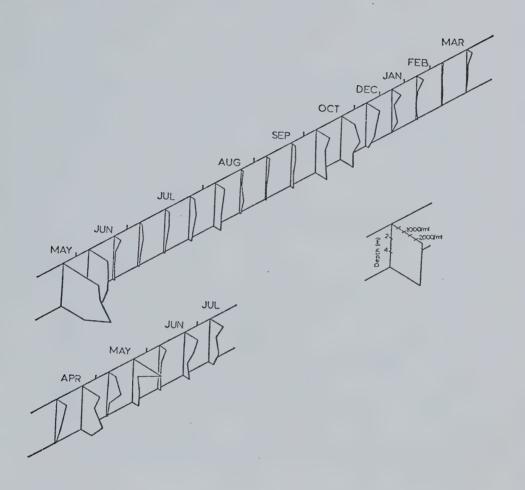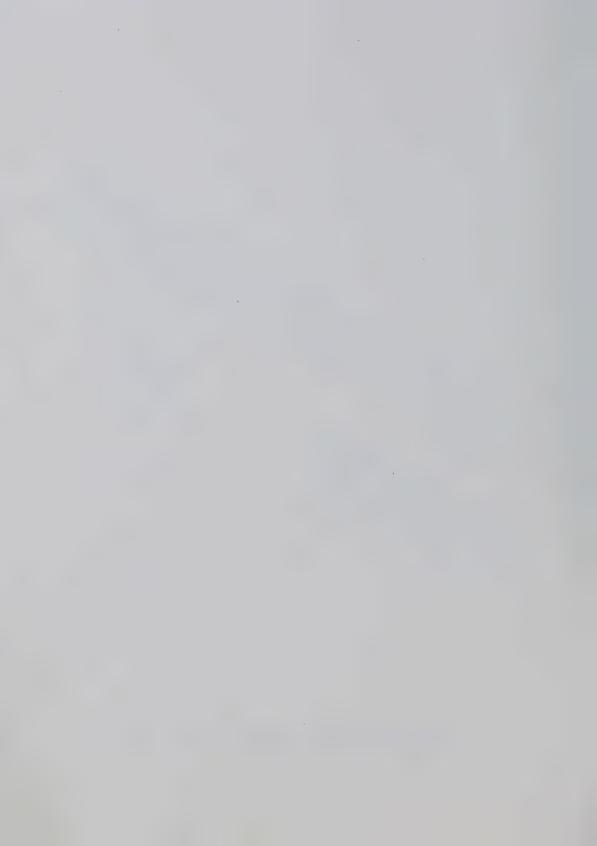
Figure 12. Vertical distribution of <u>Chlamydomonas</u> at station A.
May 23, 1975-July 2, 1976.
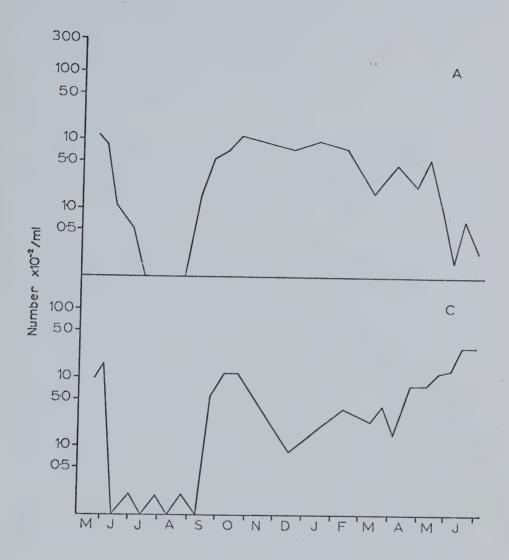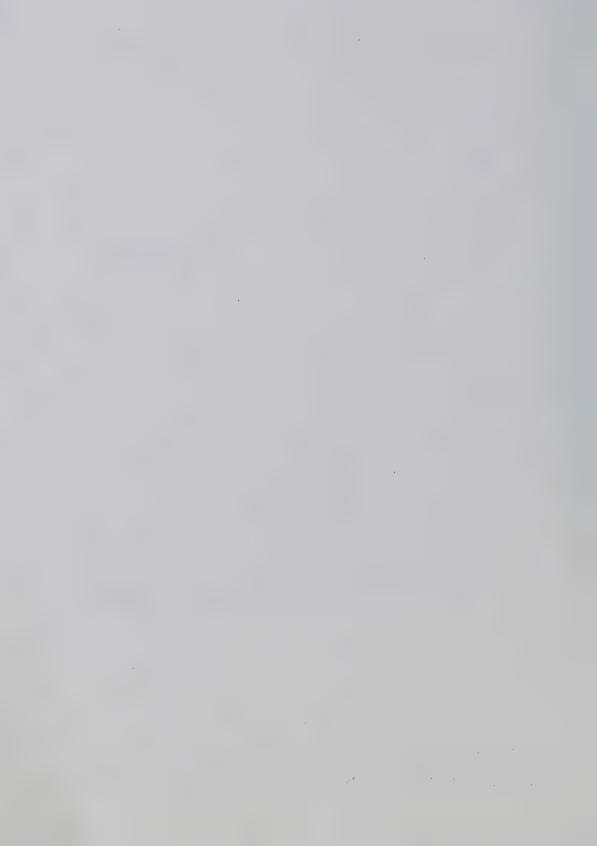
Figure 13. _Kirchneriella_ cell numbers at stations A and C, 1975-1976.

Kirchneriella showed an interesting vertical distribution during the winter months (Fig. 14), concentrating closer to the lake bottom while most of the other cells concentrated near the ice. During ice-free periods distribution was uniform.
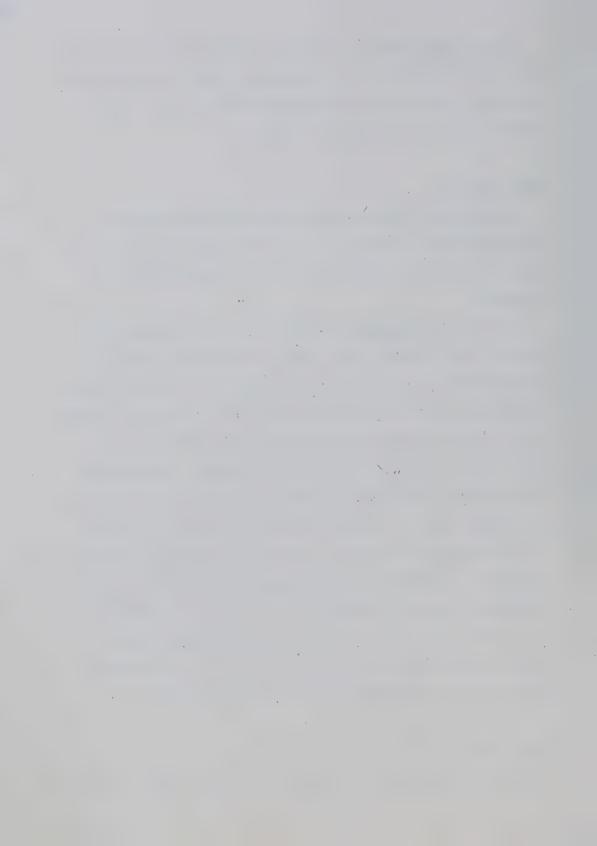
Ankistrodesmus

Ankistrodesmus was probably represented by several species during the year. The cells are long, often greater than 20μ , but narrow. Cells were usually single but were occasionaly seen in clusters.

Numbers of Ankistrodesmus dropped rapidly during late May and and early June 1975 (Fig. 15). During the remainder of June and throughout July, the numbers, approximately equal at stations A and C, declined slowly to a minimum in August, then increased to a maximum in late October. Numbers declined sharply after freeze-up and remained at low levels for the rest of the winter. Both stations showed increases during April and May 1976 but station C exhibited much higher numbers. The population density at station C appeared to be levelling off during June 1976 while the numbers at station A appeared to be increasing. Ankistrodesmus cells at station C were approximately an order of magnitude more dense than at station A during this time. For most of the year, Ankistrodesmus showed a uniform vertical distribution with the exception of late April and May 1976 when concentrations at the surface were observed.

Rhabdomonas

Rhabdomonas appeared to be a highly edible cell, approximately
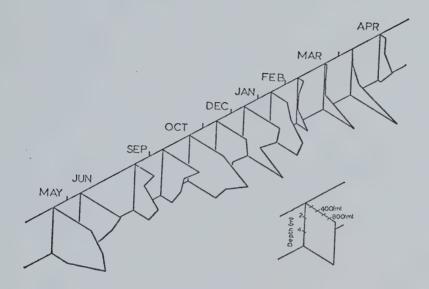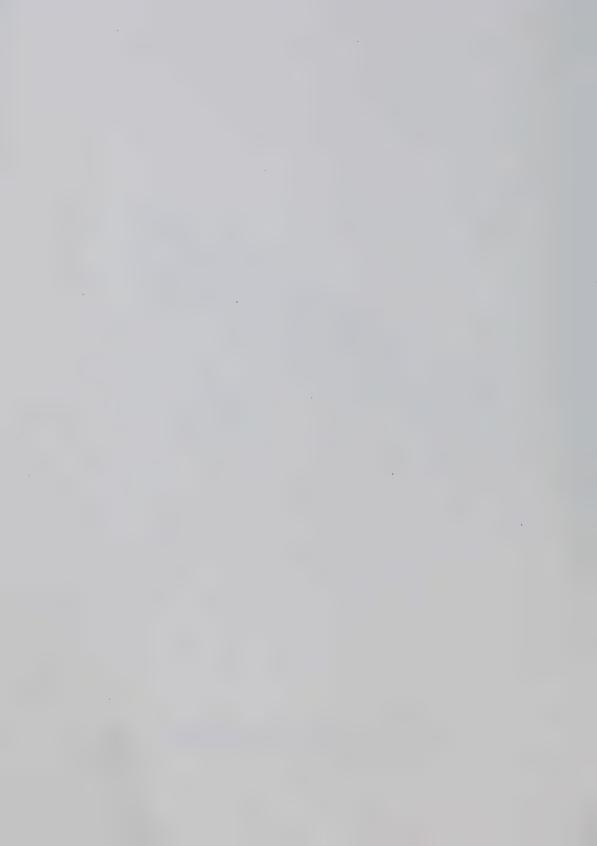
Figure 14. Vertical distribution of _Kirchneriella_ at station A.
May 23-June 6, 1975; September 23, 1975-April 27,1976.
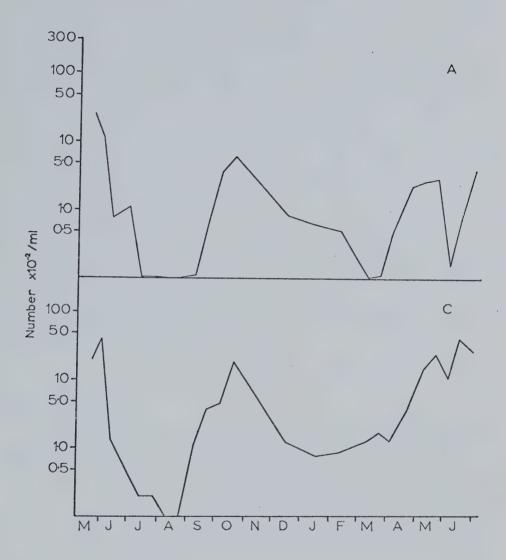
Figure 15. <u>Ankistrodesmus</u> cell numbers at stations A and C, 1975-1976.
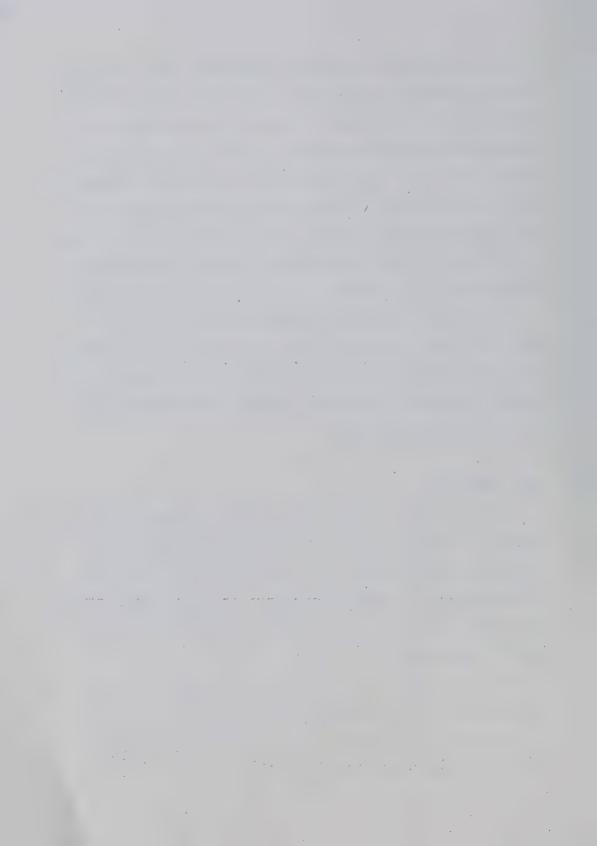
4 μ by 1 μ and existed as individual, flagellated cells. It appeared
in high numbers during spring only. When sampling began in late May
1975, the population at station A was over 1600 cells per ml but
disappeared completely by mid-June, as did the small population at
station C (Fig. 16). Until late winter 1976, populations remained at
zero with the exception of a few cells seen during late August and
early September 1975 and February 1976. The 1976 spring pulse began
in late March at station A and continued until May when the numbers
declined again. The population density in 1976 was never as high as
in 1975 but, like spring 1975, no cells were seen after June. A
short-lived pulse was seen at station C during April and May 1976 but
again, the population density was less than that at station A. The
vertical distribution was uniform with slight concentrations near
the surface during April 1976.

Small Flagellates

Because of their size, 3 μ by 1 μ , the small flagellates proved
difficult to identify but were counted because of their apparent
edibility and large numbers. The cells counted do not represent a
heterogeneous group of unidentified cells; rather, the size and form
were regular throughout the year, indicating perhaps that the cells
were of a single species.

Numbers of cells at station A declined rapidly during late May
1975 and a small population was maintained until August (Fig. 17).
In contrast, no small flagellates were found at station C during
spring and summer. Small flagellates were present at both stations
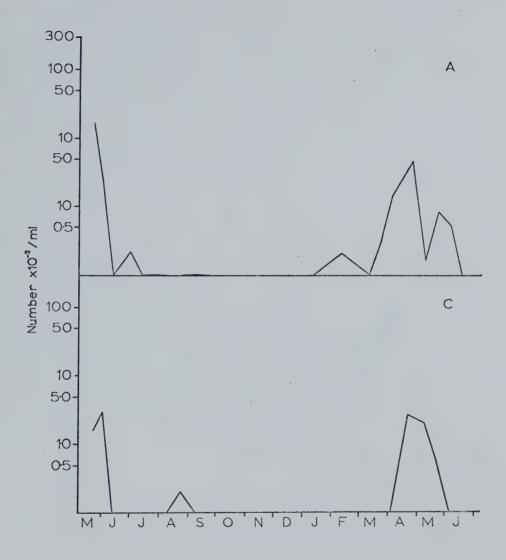
Figure 16. _Rhabdomonas_ cell numbers at stations A and C, 1975-1976.
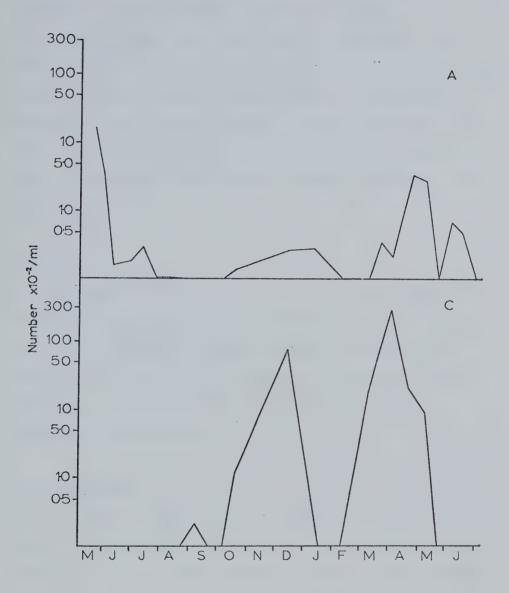
Figure 17. Small flagellates cell numbers at stations A and C, 1975-1976.

during fall and early winter, with station C supporting a much higher population. A second increase at station C, beginning in early March 1976, reached close to 30,000 cells per ml in early April. This population subsided quickly and no cells were found after early May. A second increase occurred at station A about this time, but the numbers were fewer and the population disappeared during late June 1976. The vertical distribution was uniform with the exception of late April and mid-May 1976 when cells were more concentrated near the surface.

Ochromonas

Ochromonas is 2 μ by 6 μ and elliptical in shape. During the study period Ochromonas appeared at station A during late March and early April 1976, rising in numbers from zero in mid-March to a maximum of 600 cells per ml in early April; no cells were found in late April. Most of the cells were found near the surface. Ochromonas was never found at station C.

Total Edible Cells

In an effort to summarize data on phytoplankton cells, population densities of each species were summed and expressed as Total Edible Cells (Fig. 18). An obvious decrease in numbers at both stations was seen during spring and early summer 1975. Population densities at the two stations were similar. Low numbers were recorded in July and August but the populations rose quickly in autumn with station C exhibiting consistently higher population densities. The population at station C increased slowly in early winter but a sudden decrease
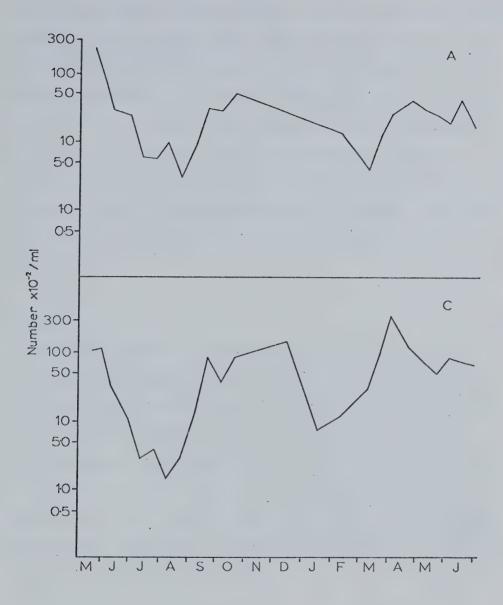
Figure 18. Total Edible Cells, cell numbers at stations A and C, 1975-1976.

was noted in January. Numbers increased again in February and reached a maximum of approximately 32,000 cells per ml in early April. The population density decreased after reaching the maximum but remained high for the remainder of spring and early summer. At station A the numbers decreased steadily during winter to a minimum of 400 cells per ml in March. The population density increased again during late winter and early spring and appeared to stabilize for the remainder of the study period. The population density at station C was consistently greater than that at station A during spring and early summer 1976.

Cyanophyta

Relative abundances of certain blue-green algae were recorded. Edmondson (1965) did not consider Cyanophyta important in his study but they are included here because of their dominance during summer months and the possiblilty, to be discussed later, of them acting as a food source. Three major cell types were quantified; Anabaena, a filamentous blue-green with round cells; Microcystis, a colonial algae with small cells tightly packed in mucilage; and Aphanizomenon-Oscillatoria, a combination of two filamentous genera with rectangular cells. Results are given in Table 4.

Anabaena

Anabaena first appeared in mid-June 1975. The population developed slowly at station A and was never rated more than "common". It had disappeared by early September. In 1976, Anabaena appeared at approximately the same time as it had in 1975. The station C

TABLE 4

Comparative abundances of Cyanophyta at stations A and C.
1 present; 2 fairly common; 3 common; 4 abundant; 5 very abundant.

Date		Anabaena	Aphanizomenon- Oscillatoria	Microcystis
23/05/75	A	---	---	---
	C	---	---	---
02/06/75	A	---	---	---
	C	---	---	---
13/06/75	A	1	---	---
	C	1	---	1
01/07/75	A	2	---	---
	C	1	1	1
14/07/75	A	3	3	3
	C	4	3	4
28/07/75	A	3	3	4
	C	5	5	5
11/08/75	A	3	4	4
	C	3	5	5
25/08/75	A	2	2	4
	C	3	3	3
10/09/75	A	2	2	3
09/09/75	C	2	5	2
24/09/75	A	1	2	2
	C	2	4	2
09/10/75	A	---	2	---
	C	1	4	2
23/10/75	A	---	2	---
	C	---	2	1
Winter 1975-76		---	---	---
07/06/76	A	---	---	---
	C	1	---	---
18/06/76	A	2	---	1
	C	2	---	---
02/07/76	A	2	---	---
	C	---	1	3

population of Anabaena, like that at station A, first appeared in mid-July 1975. However, the population at station C reached a higher density than that at A; it was rated "very abundant" in late July. The population persisted until early October. Populations were similar in 1975 and 1976.

Microcystis

Microcystis first appeared in mid-July 1975 at station C. Numbers rose quickly and cells were very abundant during late July and early August. The population declined through fall but remnants of colonies were still present in late October. Microcystis was first seen in early July in 1976 and was rated "common", indicating a rapid growth during late June. The 1975 population at station A was relatively short-lived and less dense than that at station C. It was first seen in mid-July and never rose above the "abundant" rating. No cells were found after late September. In 1976, a few cells were found in mid-June but none were found in early July.

Aphanizomenon - Oscillatoria

Filaments of Aphanizomenon and Oscillatoria did not appear until early July 1975 when they were found at station C. The population at station C reached "very abundant" levels during late July and early August, decreased during late August, but rose again in early September. The population was still "fairly common" in late October. In 1976, filaments were first found in early July. In 1975, population growth at station A was similar to that at station C but never reached the same high densities. No cells were found at

station A during 1976.

Although blue-green algae were found throughout the water column, all three groups concentrated in the surface layers. During calm weather the cells formed a thick "scum" on the surface.
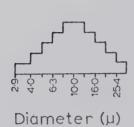
PARTICLE SIZE ANALYSIS
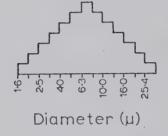
In addition to bacteria and phytoplankton counts, data on particle size and abundance were collected in order to further define and measure food resources available to rotifers. A Coulter Counter was used in an effort to determine amounts of planktonic detritus in the lake. Results are difficult to interpret for two reasons. First, there is no information available on the use of particles as food; the organic content and degree of digestibility are unknown since particles may include phytoplankton cells, large bacteria, parts of decaying zooplankton (particularly shed exoskeletons), Protozoa, disturbed sediments from the bottom, etc. The second problem arises from the limitations of the machine. In computing the diameter of a particle, the machine determines the volume of the particle and then assumes a sphaerical shape and computes the diameter accordingly. It is clear that if a long, slender particle is counted the calculated diameter will be unrealistic. It should also be noted that variation in volume is more pronounced in larger size classes than in smaller since a large diameter particle constitutes a proportionately larger volume than a small diameter particle. It was impossible in this study to determine the importance of these errors.

Results of the analyses are shown in Figure 19. One striking result was the similarity of the histograms from different depths.

Figure 19. Particle size analysis histograms from stations A and C
at depths (m) indicated. Each histogram indicates total
volume of particles in discrete size ranges.

Diameter (μ)
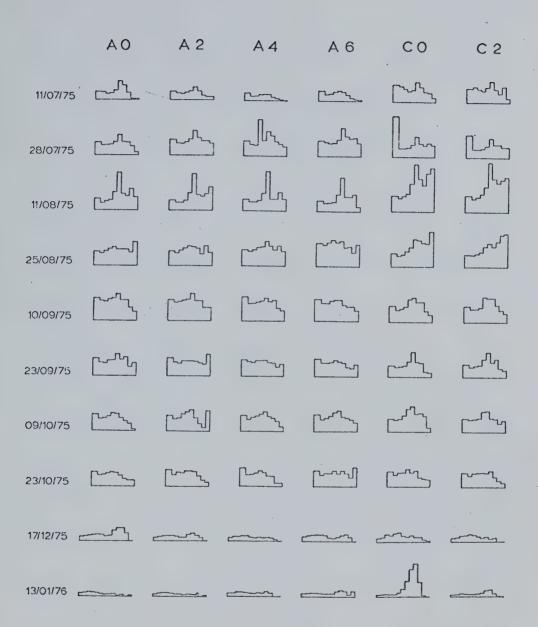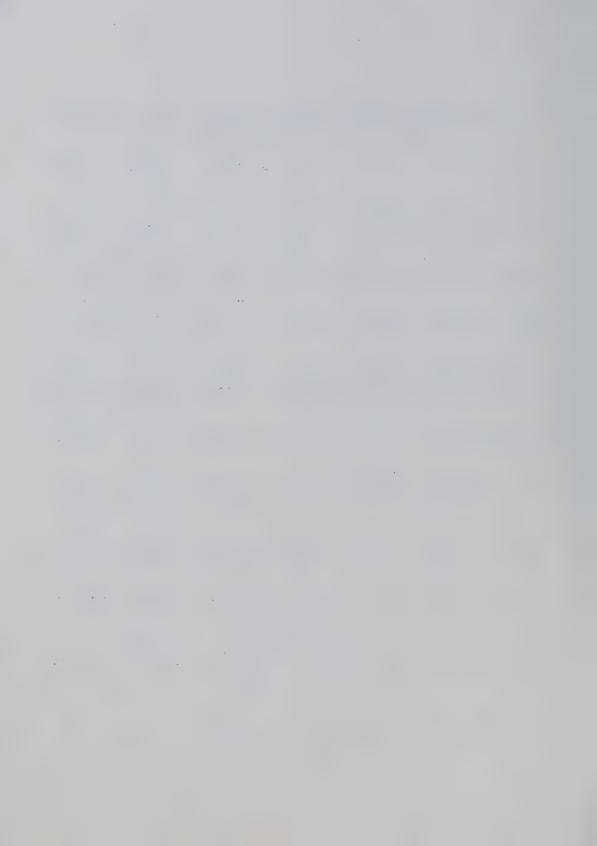
Size ranges used on Model B,
used from 11/07/75-23/10/75.
Approximately 2.6X.

Diameter (μ)

Size ranges used on Model TA II,
used from 17/12/75-02/07/76.
Approximately 2.6X.

Volume scale drawn to scale.
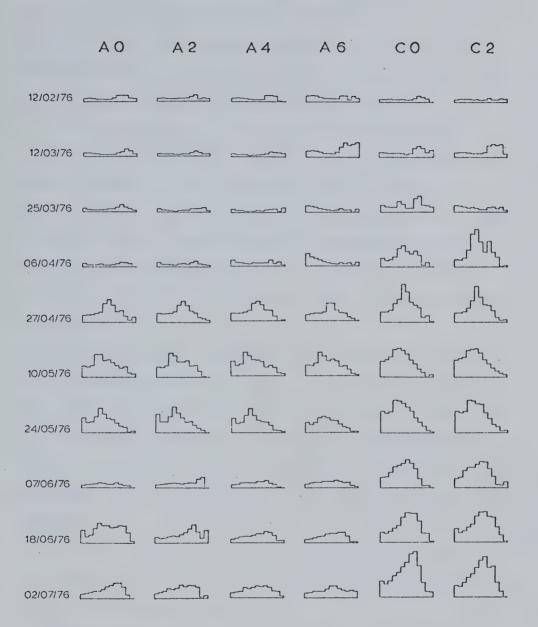
Figure 19. Continued.

Exceptions were noted at station C in mid-January when a larger volume in the 10 to 16 µ range was noted in the surface sample. Larger total volumes were also noted in March and early April 1976 at A6. In early March there was an increase in large particles while the next two dates showed a larger volume of small particles.

In mid-July, station A histograms showed low volumes with relatively even distribution across the channels. Throughout summer, volumes generally increased in all size classes. On August 11 a distinct peak was seen in the 10 to 12.6 µ size class. Total volumes stabilized again and remained high during late August and early September. A decrease was noted in late September that continued until late October with the larger size classes showing the greatest reduction.

Station C exhibited a different pattern during summer and fall 1975. A distinct peak in the 2.8 to 3.9 µ size class occurred in late July. The August 11 histograms show the same peak in the 10 to 12.6 µ size class as station A but also show a large proportion of the volume in larger size classes. Decline in total volume began in late August and, with a slight increase in early October, continued until freeze-up.

During the ice-free period total volumes at the two stations were approximately equal with the exception of August 11 when station C showed higher values.
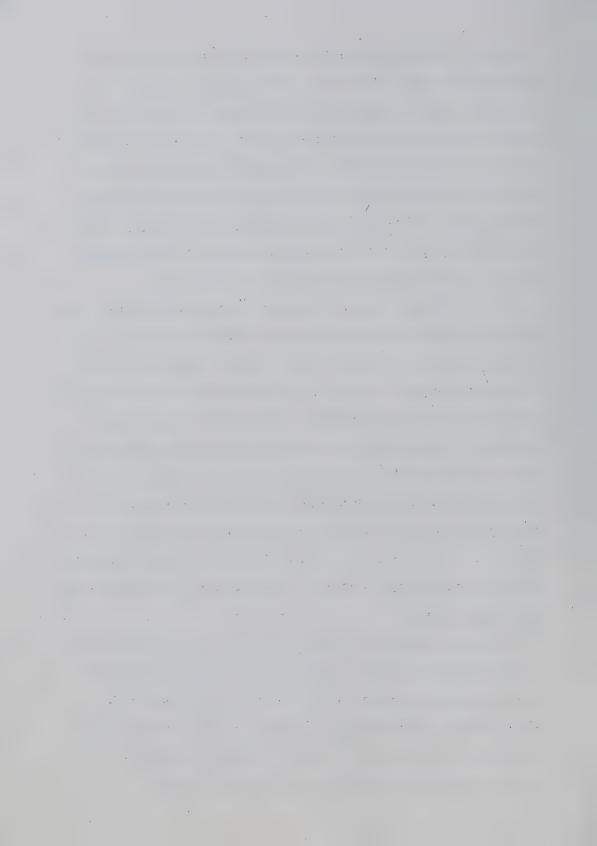
After freeze-up, the Model TA-II was used to analyze samples. This machine included the same classes as the Model B but also extended the range down to particles 1.5 µ in diameter.

After freeze-up, total volumes dropped considerably at both

stations. January and February readings were very low with the largest size channel (25 to 32 μ) often showing no volume. As mentioned earlier, a relatively large volume was recorded at CO in mid-January. This peak did not coincide with a peak in phytoplankton cells and remains unexplained. Histograms for station A during March and early April show the same low profile as the January and February data. Station C, however, showed slightly larger values during March and an obvious increase on April 6. This coincides with the observed phytoplankton increase at station C.

After break-up, volume at station A increased considerably with maximum volumes in the 5.0 to 6.3 μ and 6.3 to 8.0 μ ranges. This pattern persisted until early June. Station C maintained higher volumes than station A during this time but the maximum volumes were recorded in the same size ranges. Total volume dropped sharply at station A during early June. The volume increased again during late June and early July but maximum values were recorded in the 8.0 to 16.0 μ size range. Station C did not show a decrease in volume during early June but did show the same shift from maximum values in the 5.0 to 6.3 μ and 6.3 to 8.0 μ size classes to maximum values in the 8.0 to 16.0 μ range. During June and July 1976, station C showed high total volumes.

In general, changes in total volume were associated with changes in phytoplankton densities. High volumes in smaller size ranges during spring and fall were accompanied by peaks in the small phytoplankton cells and high volumes in the larger channels during summer and early fall were accompanied by Cyanophyta blooms. No obvious correlation with bacteria populations was noted.

CRUSTACEAN ZOOPLANKTON

Eight species of planktonic crustaceans were identified from
Hastings Lake. The cladocerans were represented by Daphnia pulicaria
Forbes, Diaphanosoma leuchtenbergianum Fischer, Bosmina longirostris
O. F. Muller, and Chydorus sphaericus O. F. Muller. The copepod
fauna consisted of two calanoid species, Diaptomus oregonensis
Lilljeborg and Diaptomus siciloides Lilljeborg, and two cyclopoid
species, Cyclops vernalis Fischer and Cyclops bicuspidatus thomasi
Forbes. The following section describes distribution and abundance of
these crustaceans in Hastings Lake during the study period.

Chydorus sphaericus

Chydorus sphaericus appeared during late summer in Hastings Lake
(Fig. 20). A few individuals were found during May and June 1975
and May 1976 but were numerically insignificant compared to July and
August populations. Chydorus was never found under the ice. The
major pulse began in late July and increased rapidly to a maximum in
August at all stations. Populations at stations A and B were similar
in their development, reaching approximately the same numbers and
declining at the same rate during September and October. The population
at station C also developed during July and August 1975 but never
reached the numbers observed at stations A and B. The station C
population declined during late August but, in contrast to the main
basin population, rose again during September to a maximum in mid-
October.

Chydorus did not show any depth preferences during summer although
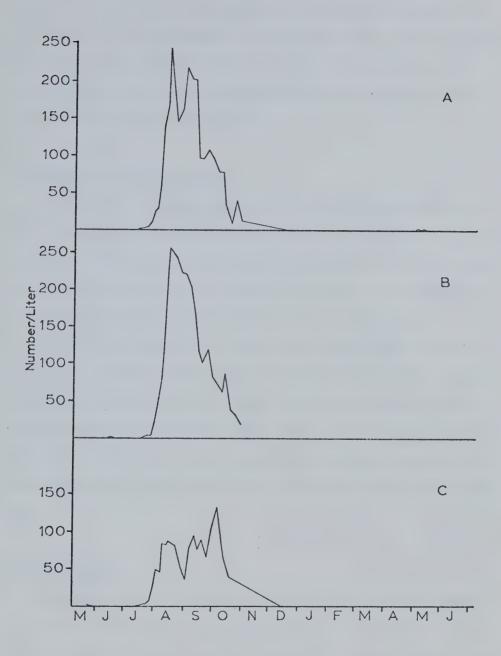
Figure 20. Population density of <u>Chydorus</u> <u>sphaericus</u> at stations A, B, and C. 1975-1976.

a slight concentration in deep water was observed on September 14, 1975 (Fig. 21). On this day the water column showed both temperature and oxygen concentration gradients. The surface water was 3 C° warmer than the bottom and was 130% saturated with oxygen, while the bottom metre was only 40% saturated.

Diaphanosoma leuchtenbergianum

During 1975, D. leuchtenbergianum was a mid summer species. It first appeared in early July samples and reached a maximum during August (Fig. 22). Populations at stations A and B were similar with respect to time of appearance, rate of growth, and density. The station C population reached a greater density than did the main basin populations; it appeared to increase faster than those at stations A and B and reached maximum numbers approximately two weeks earlier. All populations showed rapid decline after reaching maximum density and had disappeared by November 1975. During 1976, Diaphanosoma was only found at station C, first appearing in mid-June, approximately two weeks earlier than in 1975. Depth distribution was uniform (Fig. 23).

Daphnia pulicaria

Population curves for Daphnia pulicaria from stations A, B and C are shown in Figure 24. Daphnia was present at all stations when sampling began in late May, 1975. During early June, stations A and B experienced a rapid increase in numbers with maxima in mid-June. Numbers declined quickly after the maxima but peaked again during July. The station C population reached a maximum a few days earlier than
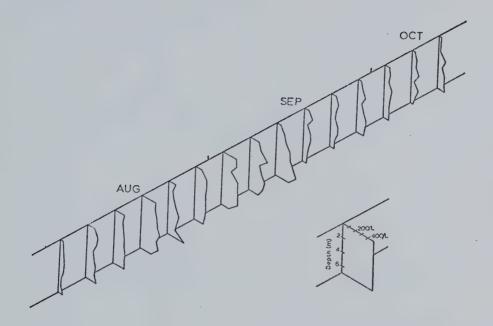
Figure 21. Vertical distribution of <u>Chydorus</u> <u>sphaericus</u> at station A.
August 8-September 13, 1975.
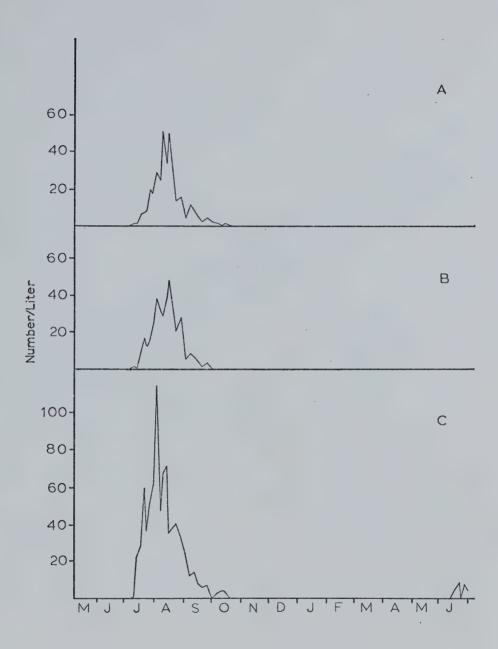
Figure 22. Population density of <u>Diaphanosoma leuchtenbergianum</u> at stations A, B, and C. 1975-1976.
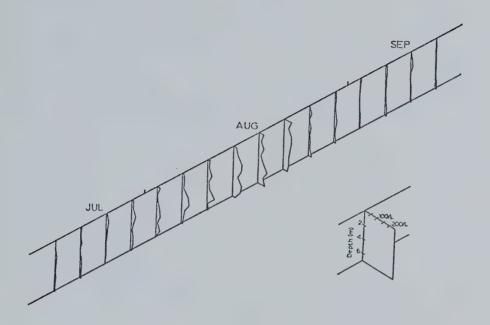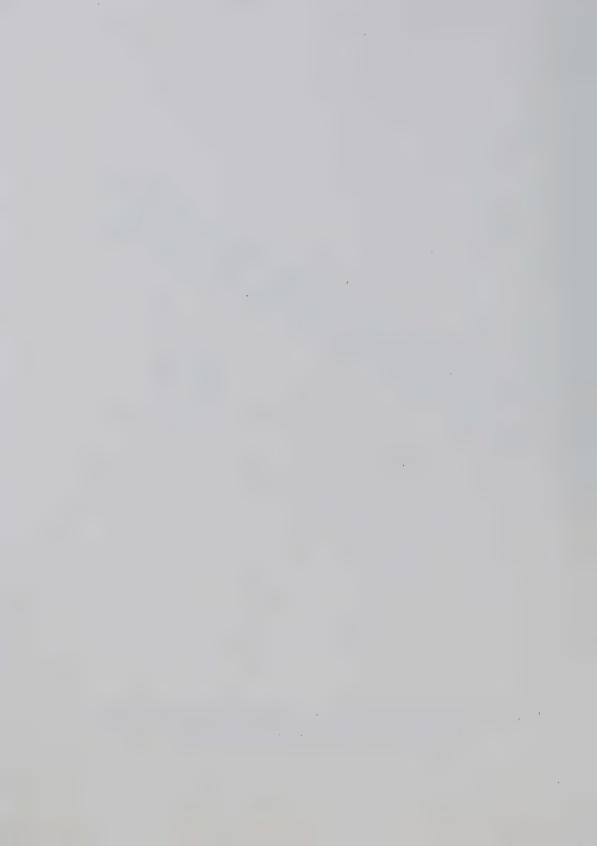
Figure 23. Vertical distribution of _Diaphanosoma leuchtenbergianum_
at station A. July 19-September 18, 1975.
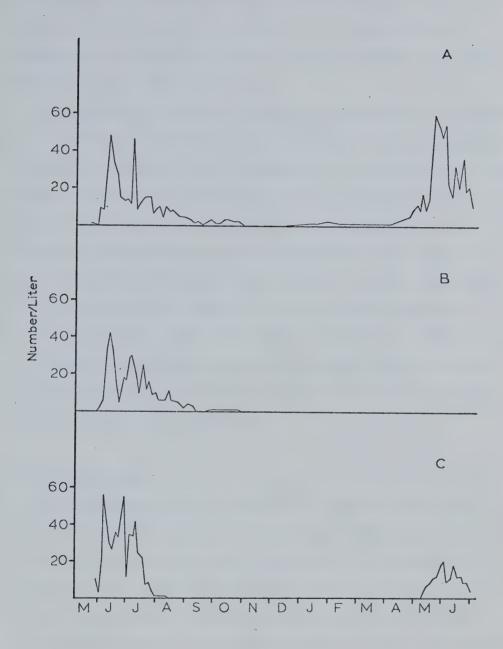
Figure 24. Population density of <u>Daphnia pulicaria</u> at stations A, B, and C. 1975-1976.

the main basin populations and the secondary peaks were stronger at station C than at either of stations A or B. The population disappeared in mid—August at station C while low numbers were found almost the entire year at station A.

The 1976 spring population increase began under the ice at station A. The population grew slowly for several weeks, but a rapid increase in numbers around the 20th of May resulted in a maximum on May 24. This maximum occurred twenty days earlier than in spring 1975, but the maximum levels were approximately equal. As in spring 1975, the population declined sharply after the maximum but peaked again ten days later. The 1976 spring pulse at station C appeared several days later than the pulse at station A, but never reached comparable numbers. At station C the 1976 maximum was less than the 1975 maximum.

Daphnia showed a slight preference for surface waters during the calm period in early July; during the rest of the year the vertical distribution was uniform (Fig. 25).

Bosmina longirostris

Bosmina longirostris was present at all stations during June 1975, but the major increase in numbers began in mid—July at station C and late July at stations A and B (Fig. 26). The population at station A dropped sharply after reaching a maximum in mid—August and then stabilized until a second major decline occurred in October. The population appeared stable during December and January but dropped quickly during February. The station B population also declined after peaking in mid—August but rose again to a maximum in early September. The fall decline began slightly earlier at station B than
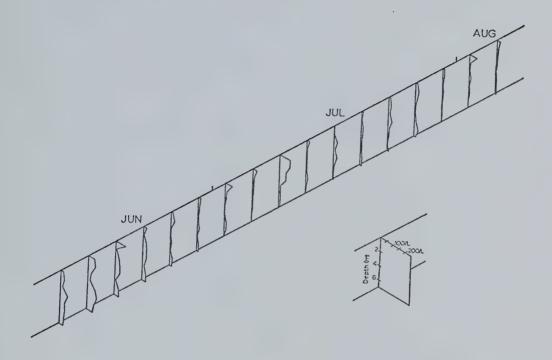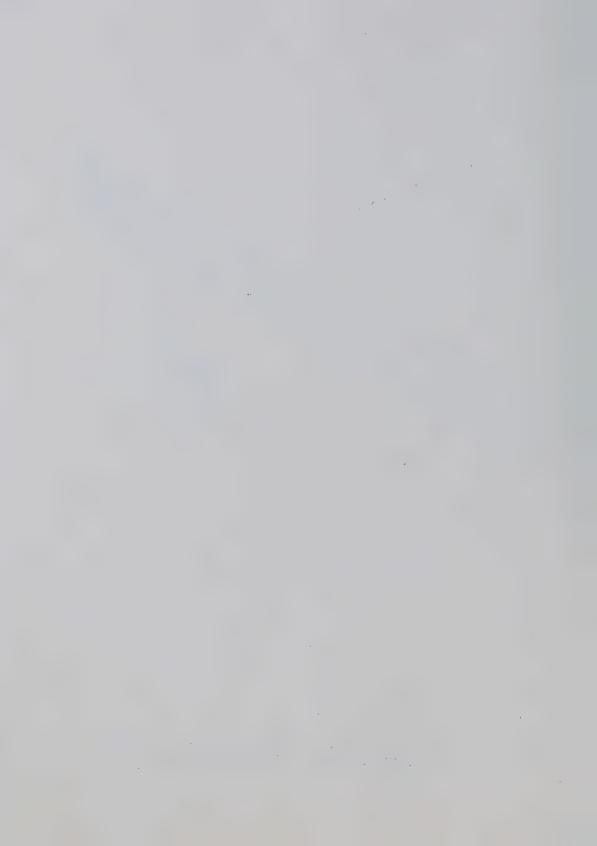
Figure 25. Vertical distribution of _Daphnia pulicaria_ at station A. June 6-August 4, 1975.
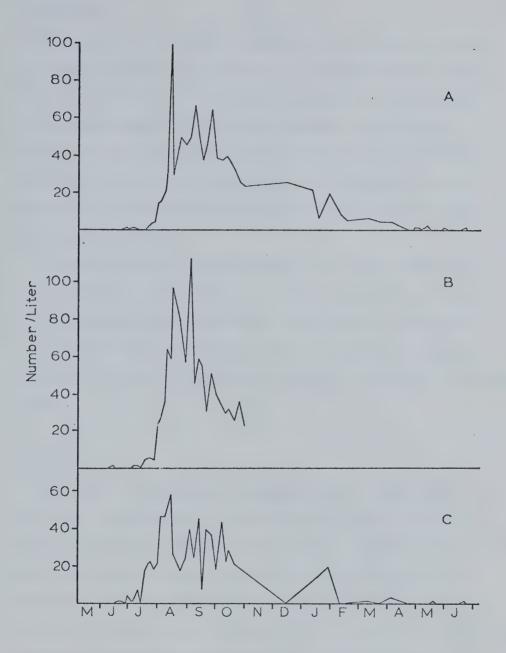
Figure 26. Population density of <u>Bosmina</u> <u>longirostris</u> at stations A,
B, and C. 1975-1976.

at station A.

The population at station C appeared similar to that at station A although the density was higher at A. The maximum during early August was followed by a decline and subsequently a stable period during September and October. Numbers dropped rapidly during November and no specimens were found in December. Except for the seemingly spurious peak in January, the winter population was low. Bosmina was not numerically important at any station during spring and early summer 1976.

During the ice-free period, Bosmina did not show a preference for any particular depth (Fig. 27). However, on December 17 under the ice, Bosmina avoided the surface of the lake and concentrated in the deeper water. In January, when the deep water was depleted of oxygen (less than 10% saturation), Bosmina concentrated at the middle depths.

Diaptomus

Two species of Diaptomus, D. oregonensis and D. siciloides, were found in Hastings Lake. The three stations showed similar population densities during the year (Fig. 28). A small pulse in early June preceded the major pulse in late June and early July. The populations fluctuated widely but maintained high densities until early September when a definite decline occurred. The populations remained low during winter and disappeared during March and April. The spring population increase in 1976 began approximately two weeks earlier than did the increase in 1975.

When the lake was well-mixed the vertical distribution was uniform
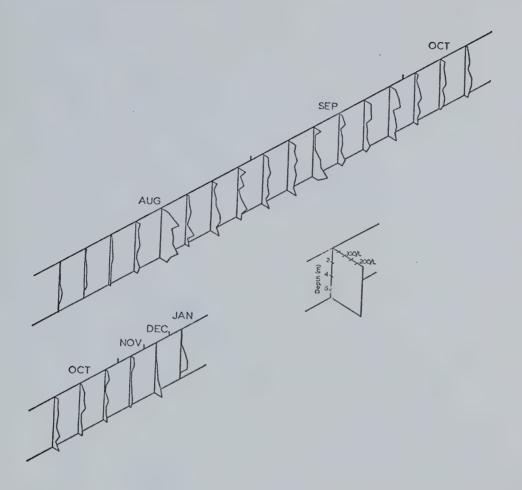
Figure 27. Vertical distribution of Bosmina longirostris at station A.
August 1, 1975-January 13, 1976.
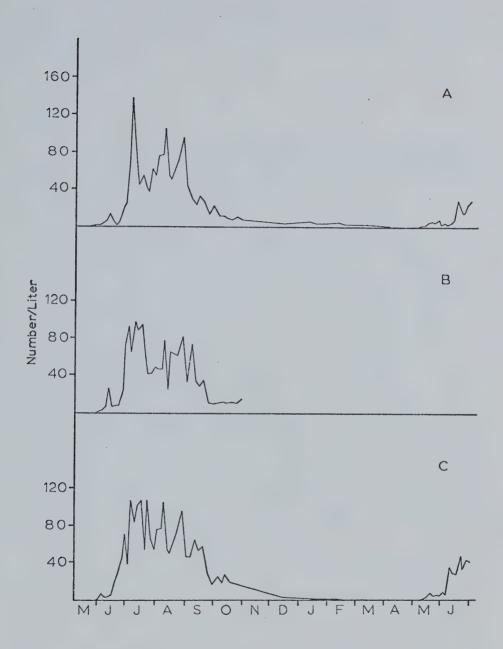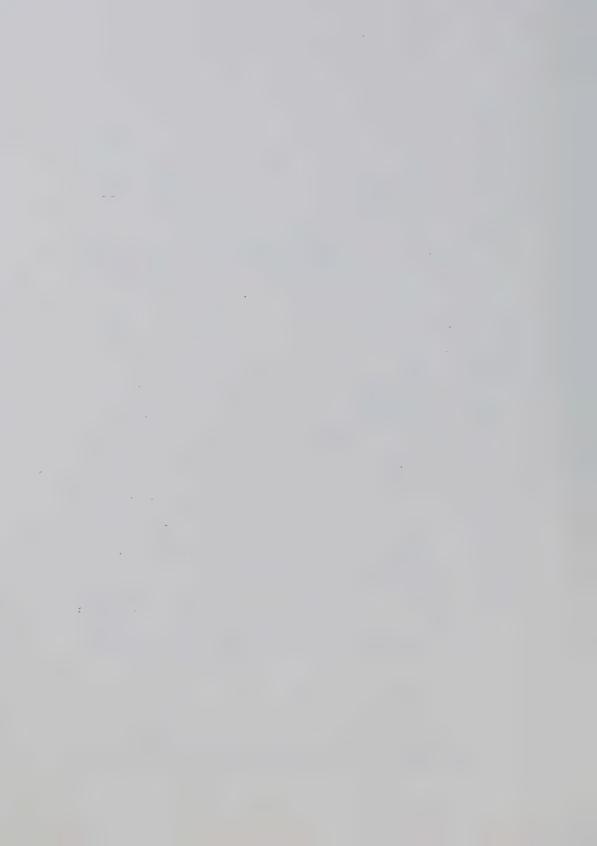
Figure 28. Population density of _Diaptomus_ at stations A, B, and C. 1975-1976.
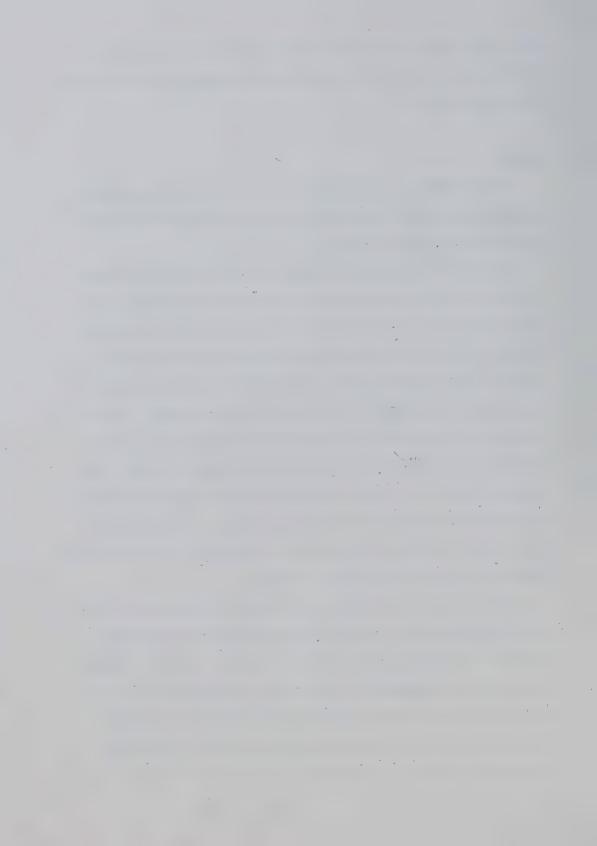
(Fig. 29). However, when the lake was calm for extended periods, ie during early July and mid September 1975, Diaptomus concentrated in the surface water.

Cyclops

The two species of cyclopoid copepods in Hasting Lake, Cyclops bicuspidatus thomasi and Cyclops vernalis were counted together and identified as Cyclops (Fig. 30).

Populations of Cyclops at stations A and B were similar. During late May and early June, densities rose rapidly to a maximum in the second week of June. Following the June maximum numbers decreased steadily, with only a small pulse at station B, until a second increase began in early August. Numbers peaked quickly in mid-August and declined again to a minimum in late September. Numbers rose again during October but declined slowly during winter. The spring increase at station A began suddenly during late April. The population grew to a maximum density in mid-May, three weeks earlier and 50% more dense than the 1975 spring maximum. Numbers dropped sharply after reaching the maximum but, in contrast to the decline in 1975, began to rise again during late June.

Population growth at station C was slightly different from that seen in the main basin. The 1975 spring maximum had already been reached by the time sampling started in late May. Numbers declined during June and remained low in July, but in contrast to stations A and B, there was no peak during late August and early September. The late fall increase (during October in the main) began during September at station C. Population density declined steadily during
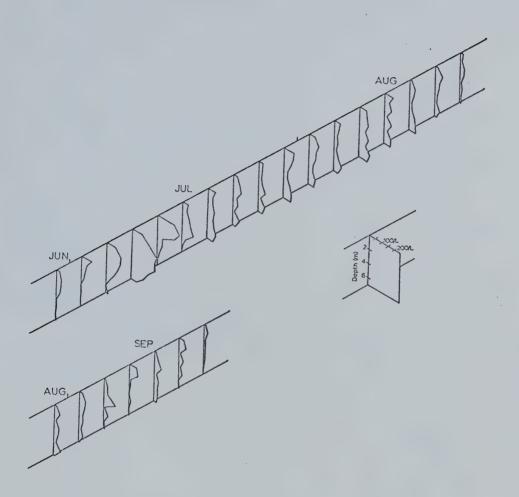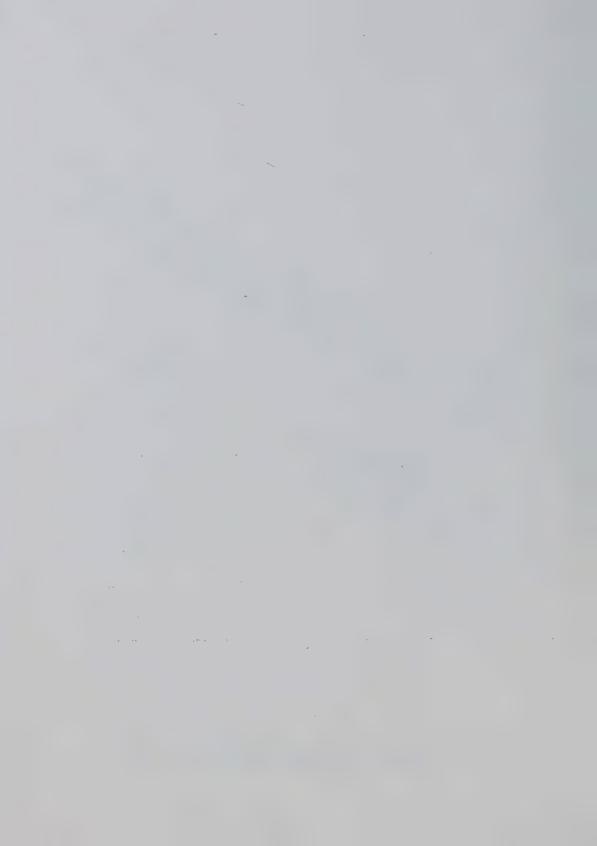
Figure 29. Vertical distribution of Diaptomus at station A.
June 28-September 28, 1975.
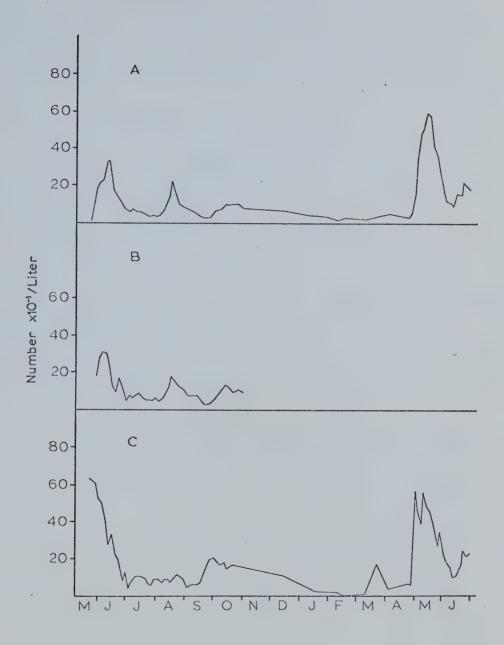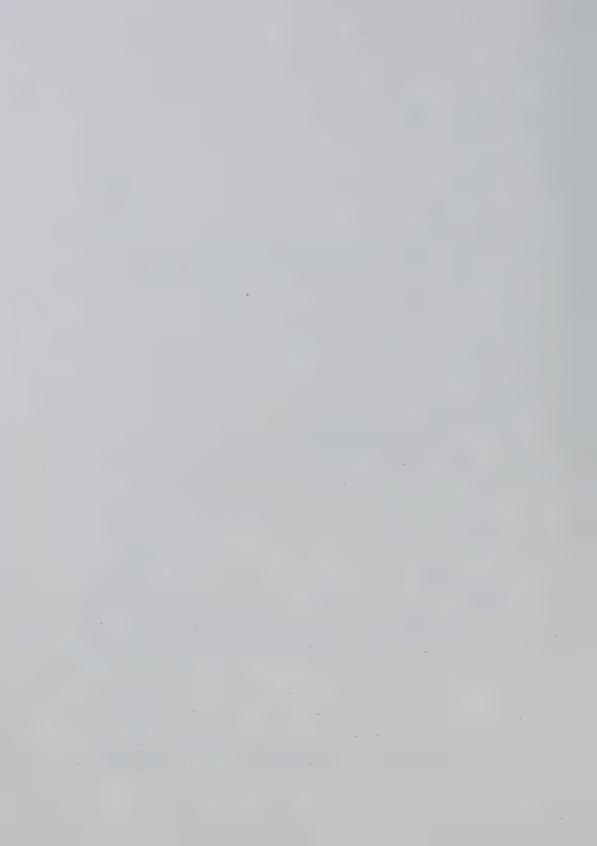
Figure 30. Population density of <u>Cyclops</u> at stations A, B and C. 1975-1976.

winter to a low in February. A pulse occurred during March but was short-lived. As in 1975, the spring pulse of 1976 began earlier at station C than at station A. After a decline during May and June, the population at station C, like that at station A, began to increase again.

Cyclops did not show a preference for any depth during the ice-free period. In December Cyclops concentrated at a depth of five metres at station A, but as the oxygen concentration dropped in the lower depths, the majority moved into surface waters.

Additional information concerning cyclopoid populations in Hastings Lake was obtained from data acquired during a detailed study of seven prairie parkland lakes (D. N. Gallup, unpublished data). Quantitative samples from station A were collected approximately monthly throughout the sampling period. It was impossible to identify the first three copepodite instars at the specific level so the counts were lumped into copepodites I-III. The IV, V, and adult instars were identified as Cyclops bicuspidatus thomasi or Cyclops vernalis. Figure 31 A shows the populations of the three groups. During 1975, copepodites I-III were most numerous in spring with peaks in mid-summer and autumn. Numbers declined through winter but increased rapidly in spring, 1976. Cyclops vernalis was most abundant during summer and early autumn, 1975, with low population densities during winter and spring 1976. The population density of C. bicuspidatus thomasi fluctuated during spring and summer 1975 and a small increase was seen during winter. A very strong increase was recorded during spring 1976.

It is generally assumed (McQueen, 1969; Anderson, 1970) that
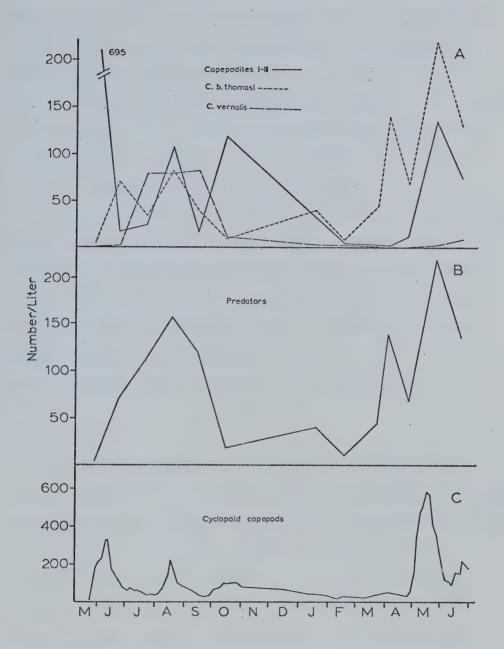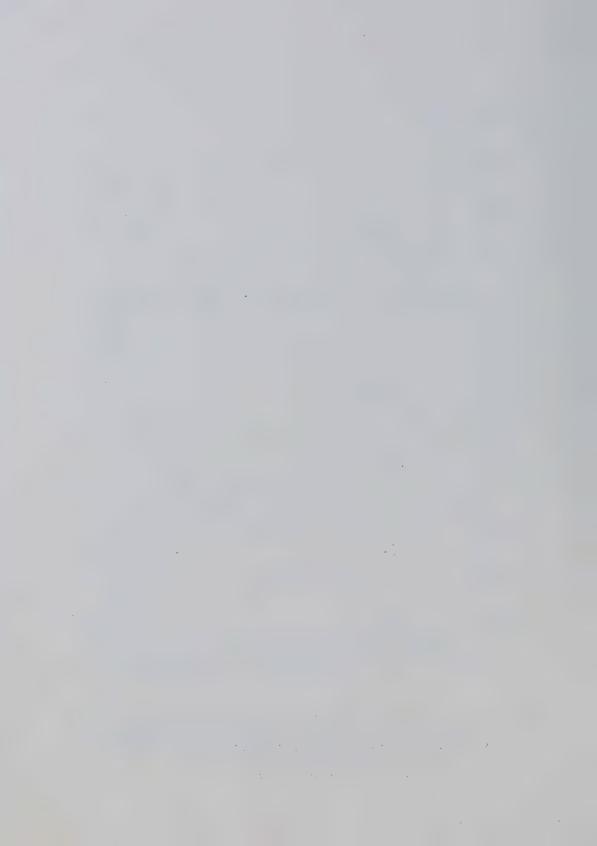
Figure 31. A. Numbers of cyclopoid copepodites I-III, C. bicuspidatus
thomasi, and C. vernalis. B. Numbers of predators.
C. Numbers of all cyclopoid copepods. All at station A.
A and B from Gallup (unpublished data).
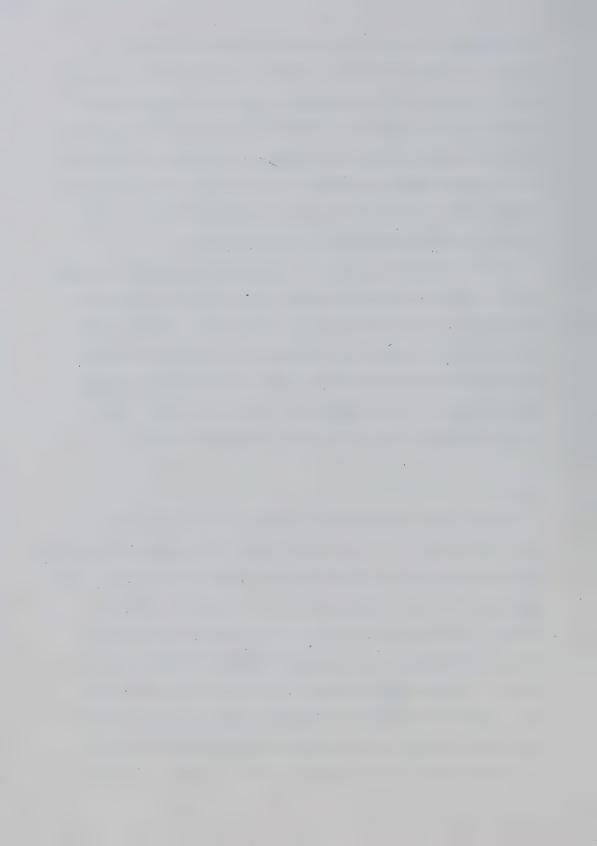
late copepodite and adult stages are the predaceous forms of cyclopoid copepods. Therefore, densities of the last two copepodite instars and adults of C. bicuspidatus thomasi and C. vernalis were summed to give an estimation of the density of predators (Fig. 31 B). Figure 31 C shows the density of Cyclops for comparison. The validity of this assumed predatory behaviour and composition of the predatory community will be discussed in predation sections of the chapters entitled "Population Dynamics" and "Cyclomorphosis".

Density of predators was low in May but increased steadily through June and July to a maximum in August. Numbers dropped slightly in September and a major decline was noted in October. During winter numbers remained relatively low. Densities of predators in spring and summer 1976 were approximately equal to densities of C. bicuspidatus thomasi since C. vernalis was rare at this time. Thus, predatory density was high from early April through June.

Nauplii

Copepod nauplii showed the same pattern of occurrence at all three stations (Fig. 32). During late May 1975, populations, consisting almost exclusively of cyclopoid nauplii, were declining rapidly. This correlated with a simultaneous increase in numbers of cyclopoid copepods. After minima in mid-June, populations increased slowly through late June and July, showing considerable fluctuations in density. A large number of calanoid nauplii were present at this time. Populations started to decline in August and continued this trend through autumn. Numbers remained very low under the ice.

In April 1976 nauplii increased greatly in numbers. A maximum
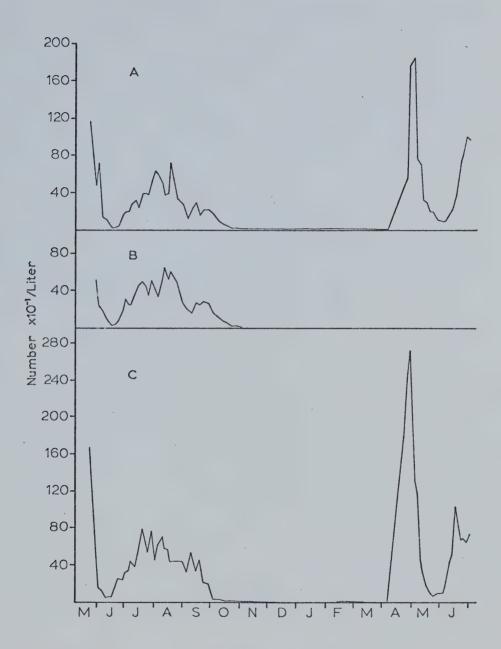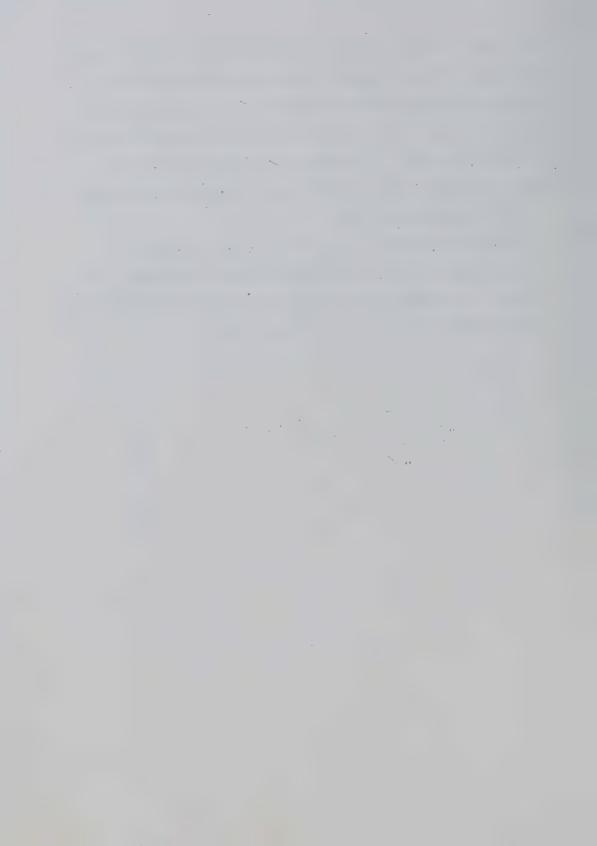
Figure 32. Population density of nauplii at stations A, B, and C. 1975-1976.

was reached on May 4 at both stations A and C with station C having
the highest population density. After the maximum was reached,
numbers declined as quickly as they rose. As in spring 1975, the
population during the initial pulse was composed almost exclusively
of cyclopoid nauplii. The second pulse of 1976 (including many
calanoid nauplii) began on June 11, approximately two weeks earlier
than the second pulse of 1975.

During mid-July 1975 and immediately after ice break-up
1976, nauplii were rare in deep, oxygen-depleted waters (Fig. 33).
However, in late July and early August 1975 nauplii were concentrated
in deeper water that was unsaturated with oxygen.
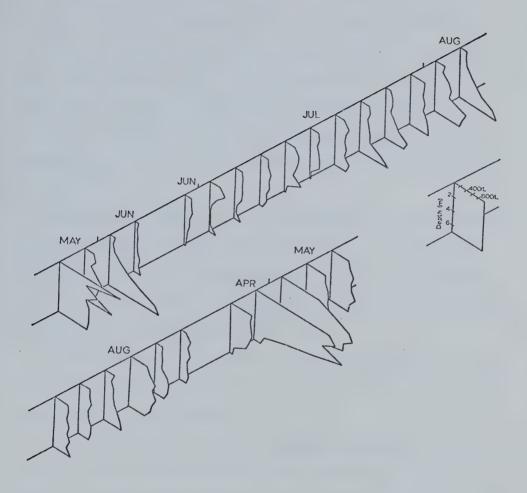
Figure 33. Vertical distribution of nauplii at station A. May 23-
June 6, 1975; June 28-August 31, 1975; April 27-May 10,
1976.

EGG DURATIONS

This section will present data on the duration of development of rotifer eggs obtained in this study and discuss the use of data from Amren (1964a). Least squares regression lines used in equation (1) are shown in Figure 34. Information on the rate of development of Keratella cochlearis, Brachionus angularis, and Pompholyx sulcata was obtained in this study. Raw data are presented in Appendix I.
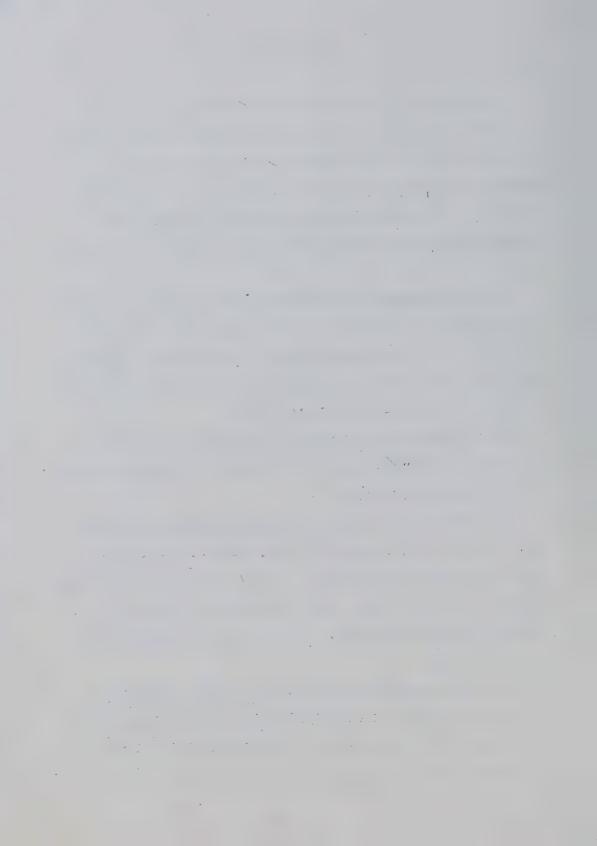
Keratella cochlearis was the easiest animal to culture; a total of 11 durations were recorded at temperatures of $10^{\circ}C$, $11^{\circ}C$, $20^{\circ}C$, and $20.5^{\circ}C$. Data for K. cochlearis were also used for K. earlinae due to the lack of data on K. earlinae and to the close relationship of these two species (Ruttner-Kolisko, 1974).

Seven durations were recorded for Brachionus angularis, 3 at $15^{\circ}C$ and 4 at $19^{\circ}C$. This species was difficult to work with as eggs were often attacked by fungus.

Four durations were recorded for Pompholyx sulcata, 2 at $19^{\circ}C$ and 2 at $22^{\circ}C$. This species also proved difficult to work with. Over forty animals were observed to lay eggs but only four lived long enough for the egg to hatch. This same problem was reported by Edmondson (1960) who was unable to record a single duration despite observing 15 eggs.

Experiments were also performed with Polyarthra dolichoptera and Filinia longiseta but produced confusing results. While duration of development for the other species tested was precise, results for F. longiseta and P. dolichoptera showed a wide range of values for
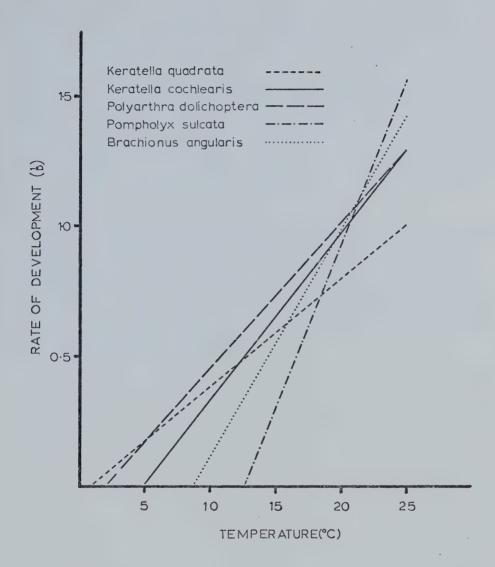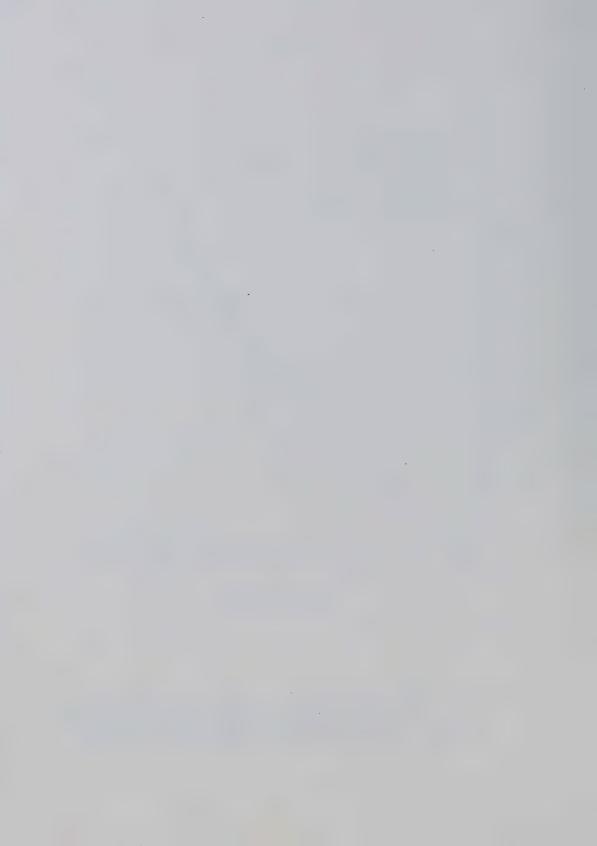
Figure 34. Least squares regression line for rate of development of
eggs of <u>Keratella</u> <u>cochlearis</u>, <u>Keratella</u> <u>quadrata</u>, <u>Brachionus</u>
<u>angularis</u>, <u>Pompholyx</u> <u>sulcata</u>, and <u>Polyarthra</u> <u>dolichoptera</u>.
Data for <u>K. quadrata</u> and <u>P. dolichoptera</u> from Amren (1964a).

any particular temperature. When eggs of these species were first
laid a considerable amount of structure was often visible within the
egg; the developing mastax was particularly noticeable. It was
also noted that the degree of development was different in freshly
laid eggs; some showed no development while others appeared ready to
hatch. It appears, therefore, that a variable amount of development
takes place in the female before the egg is laid, thereby causing the
wide spread of observed values. Because of this problem results
were not used.

Data from Amren (1964a) were used in equation (1) for Keratella
quadrata and Polyarthra dolichoptera. Amren's data were obtained
from animals collected from Spitzbergen Island; therefore, the use of
his data in my study assumes no difference in egg durations between
the widely separated populations.

ROTIFERS

A total of seventeen species of planktonic rotifers were found
in Hastings Lake. A few species of unidentified bdelloid rotifers
and a few Lecane were found but were not considered euplanktonic and so
were ignored. This section describes distribution and abundance of
individual species and includes notes on their relationships with
selected environmental factors. Birth rates are described for those
species that carry eggs and cyclomorphosis patterns are described
for the three dominant species of Keratella.

Conochilus unicornus Rousselet

Conochilus unicornus was the only colonial rotifer found in
Hastings Lake. Ruttner-Kolisko (1974) describes the colonies as
containing five to twelve individuals, but colonies of up to twenty
individuals were occasionally seen. Horkan (1971) also noticed
colonies of greater than twelve individuals. High numbers of in-
dividuals in a colony may be indicative of a rapid rate of repro-
duction (Ruttner-Kolisko, 1974). The trophi of C. unicornus is
malleoramate with many small teeth on the unci. Pejler (1957a)
suggests that C. unicornus eats particles with diameters less than
10 μ and Naumann (1923 in Pejler, 1957a) noted C. unicornus ingests
particles smaller than those used by species of Keratella, Filinia
and Kellicottia.

Conochilus unicornus was first collected from the main basin in
early June 1975 (Fig. 35). Numbers at both stations A and B remained
low for several days but a sudden increase was noted in mid-June.
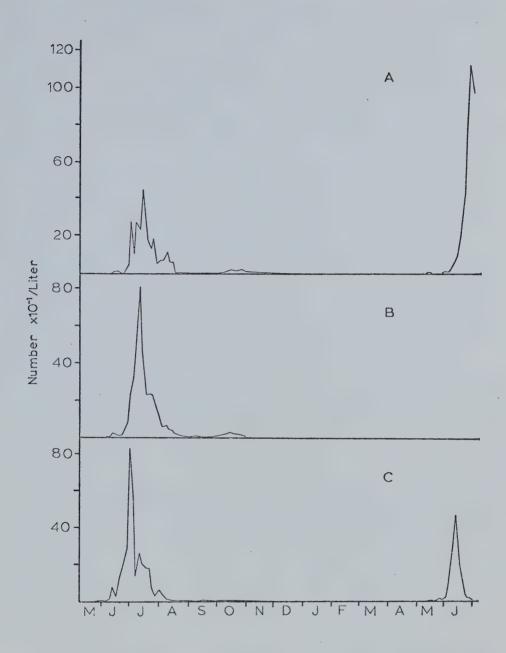
Figure 35. Population density of _Conochilus unicornis_ at stations A, B, and C. 1975-1976.

The pulse at station B continued to a maximum in mid-July while the population at station A experienced a few setbacks during early July, reaching a maximum several days after the maximum at station B. During July numbers at station B were higher than numbers at station A. The vertical distribution graph of C. unicornus (Fig. 36) shows that this organism has a distinct preference for surface waters. It is possible that observed differences in population density at the two stations were a function of depth of water. A sign test (Sokal and Rolf, 1969) showed no significant difference in densities of C. unicornus in surface waters of the two stations, but the density at station A as a whole was low with respect to station B because the additional two metres of sparsely-populated water at station A reduced the average density. A sharp decline occurred at both stations immediately after maxima were reached in July. The decline continued through August but populations persisted in low numbers until October when small increases in density were noted. No specimens were found under the ice.

In 1976 C. unicornus was first seen in mid-May at station A. The population remained small during late May and early June but a rapid increase, starting the second week of June, led to a maximum in late June. The increase at station A in 1976 was two to three weeks earlier than the corresponding increase in 1975 and the 1976 maximum was twice as high as that of 1975.

Conochilus unicornus was present at station C when sampling began in late May. The population increased in mid-June and a maximum was reached on July 1, approximately two weeks earlier than in the main basin. The maximum was higher than the station A maximum but roughly

equal to the station B maximum. Numbers dropped quickly immediately
after the maximum was reached; the fall population persisted until
freeze-up with no further increases.

In 1976 C. unicornus appeared at station C at approximately the
same time as at station A. However, the increase at station C during
early June continued to a maximum in mid-June, approximately two
weeks earlier than the station A maximum. The population density
dropped quickly after the maximum and was very low by early July.
The 1976 maximum at station C was considerably lower than the 1976
station A maximum and lower than the 1975 station C maximum.

As mentioned earlier, the vertical distribution pattern (Fig. 36)
showed that C. unicornus avoided deep water during the calm period
in July when the lake had strong gradients in both temperature and
oxygen concentration. In late June 1976, when the isotherms and
isopleths showed slight gradients, C. unicornus had no depth
preferences.

It appears that C. unicornus is a warm water species. It was
found in water at 2°C during autumn but the population was obviously
declining. No numerical increases were found at temperatures below
12°C and the maximum during 1975 was found at temperatures above
20°C while the maximum in 1976 occurred at temperatures above 16°C.
Campbell (1941) found C. unicornus abundant in waters over 12°C
and noted maxima in water of 18 to 20°C. He also found the major
increases to occur from May through July. Chandler (1940) found
maxima between temperatures of 22 and 24°C and Davis (1954) found
abundant populations in a range of 15 to 22°C. In small lakes in
southern Ontario, George and Fernando (1969) found C. unicornus
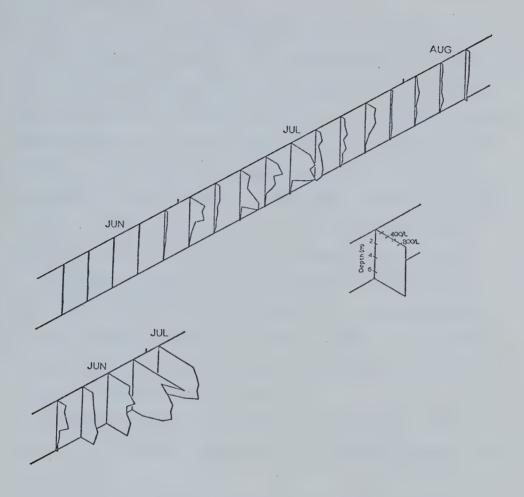
Figure 36. Vertical distribution of Conochilus unicornis at station
A. June 13-August 8, 1975; June 18-July 2, 1976.

from May until September with maxima in mid-June, a situation similar to that in Hastings Lake.

Population growth did not coincide with the edible cell concentrations. Major peaks in 1975 occurred during Cyanophyta blooms. Population growth did coincide with increasing bacteria populations and it is possible, considering the ability of C. unicornus to ingest small particles, that bacteria cells could be used as a food source. However, populations of C. unicornus dropped despite high bacteria populations. Chandler (1940) and Davis (1954) also found C. unicornus in association with blue-green algae. Both authors also reported green algae being present but did not enumerate the small cells.

Conochilus unicornus usually occurred at times and in areas of high oxygen saturation. In early July 1975, C. unicornus appeared to avoid the oxygen-depleted water near the bottom. No ill effects to the population were noted, however, when the oxygen saturation dropped to 60% in June 1976.

Conochilus unicornus was present when the Keratella species dominated, but also when crustaceans such as Daphnia, Diaptomus, and copepod nauplii were numerous.

Density of C. unicornus increased during June and July 1975 while the predator populations were also increasing. However, the populations of C. unicornus dropped during late July as predators continued to increase and were very small in August when the predators reached a maximum. The small increase in the C. unicornus population during October occurred after predator populations had declined to low levels. In 1976 the populations of C. unicornus grew slowly while predator populations were high. Rapid growth of the C. unicornus

populations occurred in late June when predators were still numerous but declining.

Conochilus natans (Selego)

Unlike C. unicornus, C. natans exist as single individuals. The mastax is malleoramate.

Conochilus natans was never common during the study period and was only found during early spring. A few individuals were seen during late May 1975 in the main basin but the population had disappeared by June 20. At station C the population had disappeared by early June. At station A in spring 1976, animals were first seen immediately after ice break-up. The population persisted in low numbers (2 to 3/liter) until mid-May. A similar pattern occurred in the north-east basin.

Conochilus natans was never found in water above 17°C and the highest densities were found in much colder water, although not under the ice. Pejler (1957a) describes C. natans as a rare "cold stenotherm" and cites 14.5°C as a maximum temperature. Pejler (1957b) also found it in eutrophic lakes during the winter and noticed it produced resting eggs in late April. In my study, C. natans occurred when the phytoplankton was dominated by edible cells.

Conochilus natans was never found in water with oxygen saturations less than 60%.

Conochilus natans was often found with large numbers of cyclopoid nauplii and Polyarthra dolichoptera. Keratella species were increasing as C. natans disappeared. During spring 1975, C. natans was present while predator populations were low, but in spring 1976, C. natans

was associated with large numbers of predators.

Filinia longiseta Ehrenberg

Considerable confusion exists in the literature on the identifi-
cation of Filinia longiseta and Filinia terminalis. Pejler (1957c),
however, has shown the two species to be distinct. The small mastax
of F. longiseta is malleoramate and Edmondson (1959) suggested the
"long, thin gullet" restricts the size of particles ingested.
Naumann (1923 in Pejler, 1957a) supported this idea by reporting that
F. longiseta feeds on "ultraseston".

During my study F. longiseta was rare at stations A and B
(Fig. 37). Specimens were found from mid-June to late October.
A short-lived pulse occurred during late July and early August 1975.
No specimens were found in the main basin during 1976. Owing to small
sample sizes no birth rates were computed for main basin populations.

Since no information exists on the duration of development of
F. longiseta eggs, the egg ratio was used as a rough approximation
of the birth rate at station C. Filinia longiseta was present at
station C when sampling began in late May 1975. The population remained
at a low density until July when a distinct increase was noted. The
egg ratio was high during early July but fluctuated considerably.
A decrease in population density in early August was correlated with
a drop in the egg ratio. A major population pulse started in early
August and reached a peak a few days later. Numbers declined in
mid-August but rose again in late August and early September. The
egg ratio was high at the outset of the major peak but declined as
the population reached the maximum and declined. The late August,
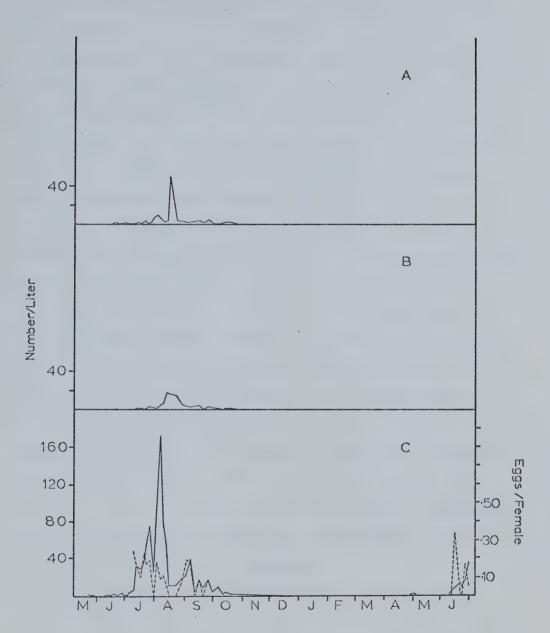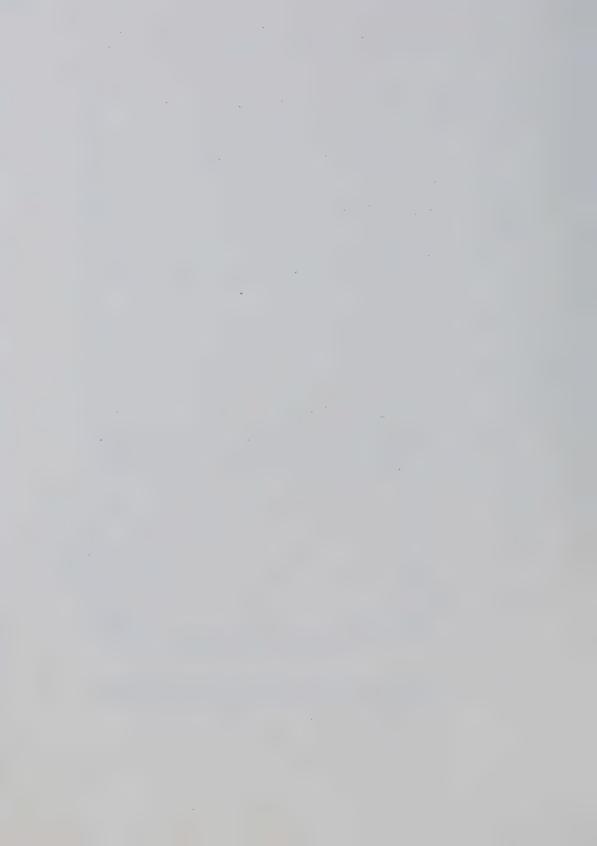
Figure 37. Population density and eggs per female of <u>Filinia</u> <u>longiseta</u> at stations A, B, and C. 1975-1976.

——— density

------ eggs per female

early September peak in population density was immediately preceded by a pulse in the egg ratio. Both the numbers and egg ratio declined during mid-September and the population persisted in low numbers until freeze-up. In 1976 F. longiseta was seen as early as late April but the population did not show any strong increases until June. The early growth stage was associated with a high egg ratio that appeared to drop very suddenly in mid-June. During the year, F. longiseta showed no particular depth preference (Fig. 38).

Although F. longiseta was found in water at 2°C, it appears to be a warm water species in Hastings Lake. No strong population growth occurred below 15°C and maxima occurred at temperatures over 20°C. This result concurs with Ruttner-Kolisko's (1974) comment that F. longiseta is a thermophile found in lakes above 15°C, usually above 20°C. Arora (1966) found F. longiseta at temperatures above 21°C. Other authors give conflicting reports on the temperature range of F. longiseta. Allen (1920) reports it present from January to July and Campbell (1941) found it in February. Chandler (1940) found this species in water from 5°C to 24°C but did not mention when maxima occurred. It may be that these authors were confusing F. terminalis, described by Ruttner-Kolisko (1974) as a cold stenotherm found at temperatures below 15°C, with F. longiseta.
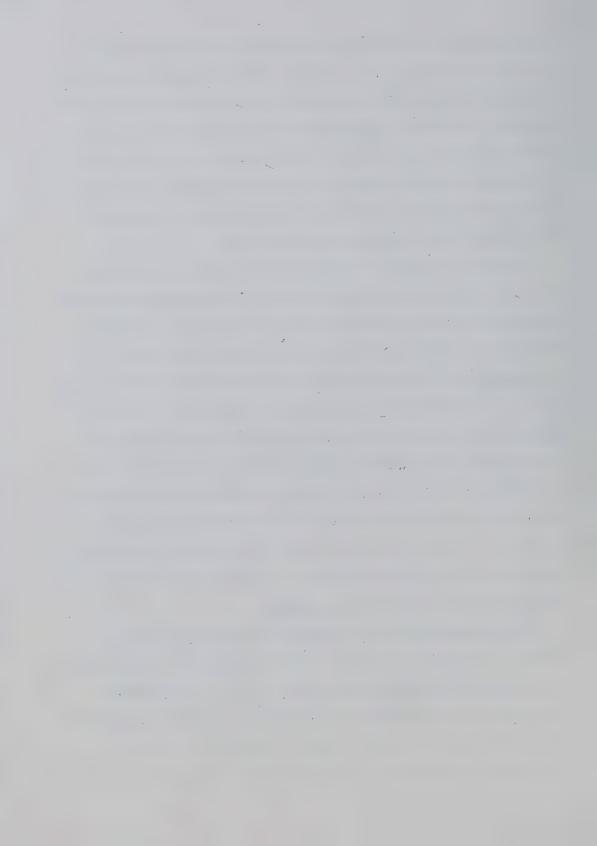
Filinia longiseta was most abundant during blue-green algae blooms. It was also present while bacteria populations were high and, considering the small size of the mastax, it may be possible that F. longiseta utilized bacteria as a food source. Population increases seen at all stations correlated well with increases in bacteria populations. Numbers of F. longiseta at station C declined sharply
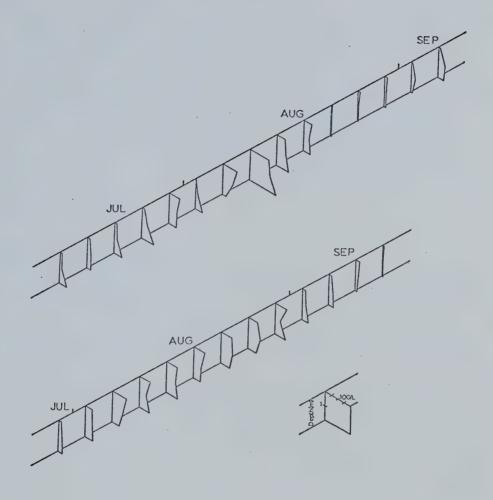
Figure 38. Vertical distribution of _Filinia longiseta_ at station
C. July 14-September 9, 1975. Upper figure.
Vertical distribution of _Brachionus angularis_ at
station C. July 28-September 18, 1975. Lower figure.

during mid-August when the bacteria population dropped. Pejler (1957b) reports F. longiseta from eutrophic waters and Arora (1966) reports it in mixotrophic ponds.

Filinia longiseta was found in waters that were oxygen-rich; the lowest reading was approximately 80% saturation.

Filinia longiseta was common during mid-summer when the zooplankton fauna was dominated by crustaceans such as Diaptomus, Diaphanosoma, and copepod nauplii (mostly Diaptomus). Filinia longiseta was most abundant at station A during July and August when the predator population was at a maximum.

Pompholyx sulcata Hudson

Pompholyx sulcata possesses a malleoramate mastax with many teeth on the unci. No literature exists on its feeding habits but the size and type of mastax would indicate it grinds small phytoplankton cells and detritus.

A small population of P. sulcata was present in the main basin during late May 1975 (Fig. 39). The population density remained low until late June when it rose quickly. When the population first began to increase the birth rate was high; however, as the numbers continued to increase, the birth rate declined. The populations at stations A and B peaked during July. The maxima at station B were considerably higher than those at station A. The populations at both stations declined during late July and early August. The birth rate fluctuated considerably during this time. During late August and through September the populations appeared to stabilize somewhat. The birth rate declined during late August and remained low through September. A second
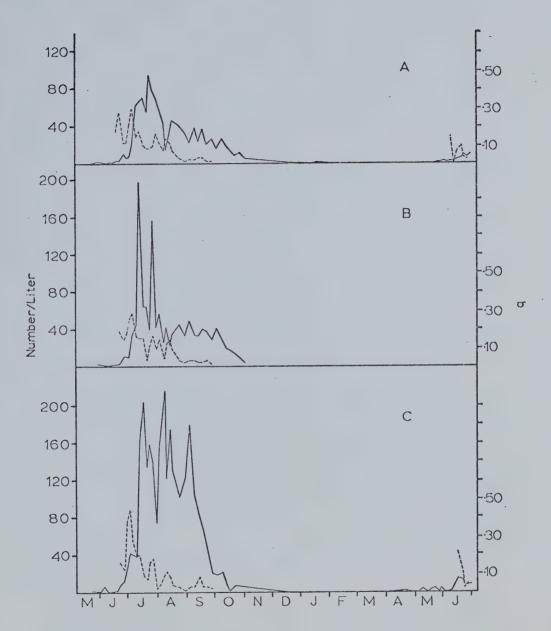
Figure 39. Population density and birth rate of _Pompholyx_
sulcata at stations A, B, and C. 1975-1976.

———density

------birth rate

major population decline was seen at stations A and B during early October. Numbers were quite low at freeze-up but the population persisted at station A until January. Pompholyx sulcata reappeared in mid-May 1976 and persisted in low numbers until early June when a slight increase was seen. Birth rates were relatively low but fluctuated widely.

The population at station C developed similarly to populations in the main basin. A major increase was noted during late June and early July that was accompanied by a steadily decreasing birth rate. From mid-July through mid-September the population showed three major peaks. Each period of decline was accompanied by an increase in the birth rate. The final decline occurred in late September and the population disappeared in November. The population at station C during May and June 1976 was similar to that at station A.

Vertical distribution of P. sulcata was uniform when the lake was well-mixed (Fig. 40). During warm, calm days of July and August, however, P. sulcata occasionally preferred deeper water. In early July when the deep water was largely depleted of oxygen, the population concentrated immediately above the point of severe depletion, in areas of 50 to 60% saturation. In late July and in August, the population concentrated in the deepest water where the oxygen was above 60% saturation.

Pompholyx sulcata was present over a range of temperatures from $0^{\circ}C$ to $24.5^{\circ}C$. Due to a very long duration of development below $12^{\circ}C$ numbers decreased when the temperature was $12^{\circ}C$ or lower. Rapid population growth did not occur until the temperature was near $20^{\circ}C$. These results compare favourably with those of Pejler (1957b)
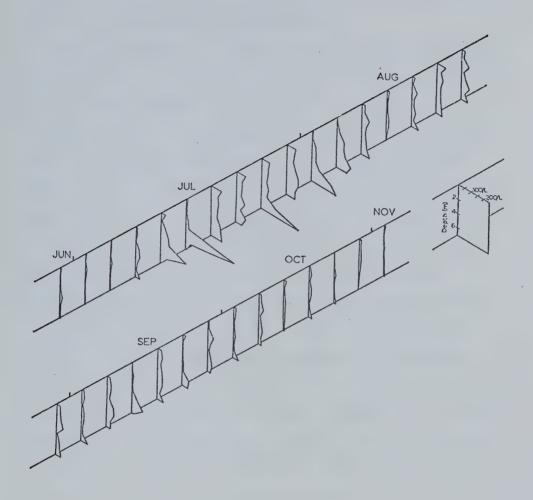
Figure 40. Vertical distribution of Pompholyx sulcata at
station A. June 28-November 2, 1975.
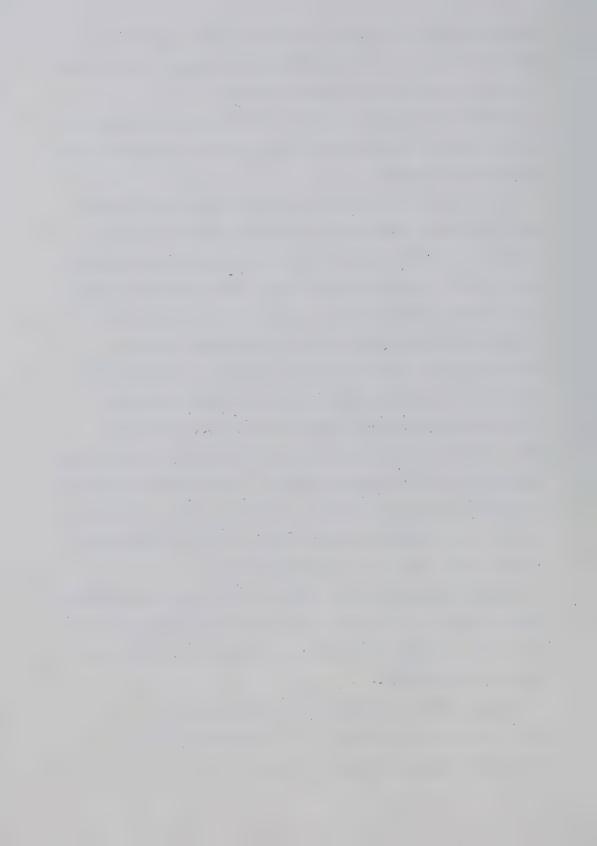
who found maxima of P. sulcata in summer and small populations in November. George and Fernando (1969) found P. sulcata during May and September in a small lake in southern Ontario.

Numbers of P. sulcata in Hastings Lake showed rapid increase and maxima during the blue-green algal blooms and were low when the edible cells were most dominant.

Figure 41 shows the relationship between temperature and birth rate. Points are widely scattered; however a "border" of points, indicated by a dashed line, can be seen extending from the low birth rates at $12^{\circ}C$ to the highest birth rate at $20^{\circ}C$. Edmondson (1965), in describing a similar graph, has attributed this border to the maximum birth rate possible under the temperatures indicated. Points lying below and to the right of the border represent birth rates that are lower due to some factor other than temperature. The border of points appears linear for most of the temperature range, indicating there is no inhibition of birth rate by temperatures as high as those encountered in the lake. The correlation coeffecient between birth rate and temperature is 0.62 ($P < 0.01$). As expected, the correlation coeffecient between birth rate and the total edible cells was low, -0.06, and not significant (N.S.).

Pompholyx sulcata tolerated a wide range of oxygen concentrations. During July 1975 it was found in water approximately 50% saturated with oxygen. In winter it was rare but present in water that was as little as 20% saturated.

Pompholyx sulcata was most abundant during warm months when crustaceans were also dominant. It was often found with Diaptomus, Diaphanosoma, Chydorus, Bosmina, and Diaptomus nauplii. Pompholyx
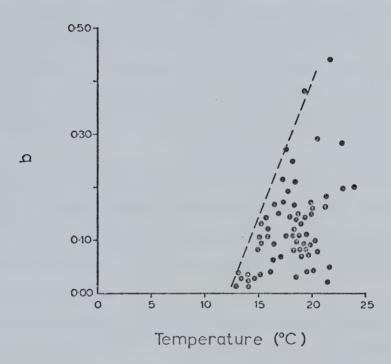
Figure 41. Relationship between temperature and the birth rate of Pompholyx sulcata. See text for details.

sulcata showed rapid population growth during July 1975 when the
predator population was increasing; however, low numbers of P. _sulcata_
in August were associated with a maximum of predators.

Testudinella patina (Herrmann)

   Testudinella _patina_ was very rare in Hastings Lake. A few
specimens were found in the main basin during early July 1975 and
a single specimen was found in mid-June 1976. Specimens were never
found at station C. Ruttner-Kolisko (1974) notes T. _patina_ occurs
"mostly at low temperatures", but all specimens were found in warm,
well-oxygenated water.

Collotheca mutabalis (Hudson)

   Collotheca _mutabalis_ is an elongate animal, partly enclosed in a
gelatinous case. Edmondson (1959) suggests the small, uncinate mastax
is adapted for trapping and tearing apart food items; however I know
of no feeding studies.

   Collotheca _mutabalis_ was rare in Hastings Lake. Specimens were
first collected in late June from the main basin. The population
grew to a maximum in mid-July and disappeared in August. A second
pulse was noted during late September and October. No specimens were
found under the ice. In 1976 a few individuals were seen in late May
and late June. The population at station C was similar to that in the
main basin but the pulse in September 1975 was more short-lived
than the pulse in the main basin. Because of small sample sizes
the number of eggs per female is only a rough estimate of birth rate.
A distinct increase in the egg ratio was noted immediately before the

population maxima in both July and October 1975.

Collotheca mutabalis was present over a range of temperatures, from 2°C to 22°C, but populations declined at temperatures below 10°C. Campbell (1941) describes C. mutabalis as a rare species with maxima at temperatures from 18°C to 21°C. Chandler (1940) found it between 15°C and 26°C and Pejler (1957a) describes C. mutabalis as a "warm stenotherm", occasionaly found below 10°C. Collotheca mutabalis was found during blue-green algal blooms in mid-summer and peaks of edible cells in late fall. Pejler (1957b) notes it is found in eutrophic situations and Chandler (1940) found it in association with both blue-green algae and Chlorophyceae. Collotheca mutabalis was only found in water with high oxygen concentrations. It was seen during dominance of the Keratella species in the fall. During June and July 1975, C. mutabalis was associated with high numbers of predators but the fall pulse was associated with low predator population densities.

Collotheca pelagica (Rousselet)

Collotheca pelagica was similar in appearance to C. mutabalis but differed in lacking eye spots and possessing a tapering foot. Like C. mutabalis, C. pelagica possesses a small uncinate mastax and was rare during the study period.

Collotheca pelagica was not found at station A until late September 1975. A maximum was reached in early November. Thus the fall population of C. pelagica was similar to the fall population of C. mutabalis. In 1976, a few specimens were found in late June. During 1975 C. pelagica was very rare at station C, although a few individuals were collected in October. In 1976 a few specimens were

collected in late May. Numbers rose rapidly during early June to a maximum in the second week of June. The population disappeared by late June. As with C. mutabalis it is difficult to interpret the egg ratio owing to the small sample sizes. However, in early June 1976 a distinct increase in the egg ratio preceded population growth at station C. As the population grew the egg ratio declined.

Although C. pelagica was found in water below 5°C, population growth did not occur in water below 10°C. Pejler (1957b) found this species during August and September. In Hastings Lake, C. pelagica was only found at times of high edible cell concentrations, when oxygen saturation was greater than 80%, and when Keratella species dominated the zooplankton community.

Synchaeta oblonga Ehrenberg

Synchaeta oblonga possesses a delicate, virgate mastax which functions to pierce and suck juices from prey items. Little is known about its choice of food but some species of Synchaeta can be cultured with Cryptomonas and small diatoms (Pourriot, 1965 in Ruttner-Kolisko, 1974).

Synchaeta oblonga was present in late May at stations A and B, but the populations disappeared by early June (Fig. 42). It was absent throughout the summer of 1975 but reappeared in mid-September. Numbers rose rapidly until a maximum was reached in late October, and by early November numbers had begun to decline until no specimens were found under the ice in December 1975. The population at station C appeared at the same time as populations in the main basin, but the maxima at stations A and B during September were much higher than the
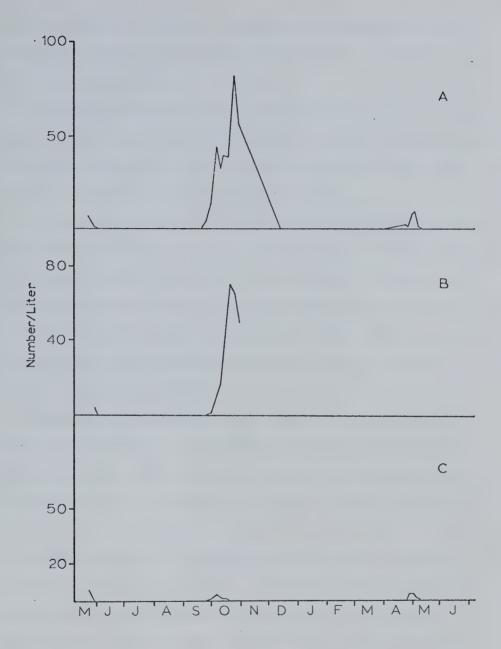
Figure 42. Population density of <u>Synchaeta</u> <u>oblonga</u> at stations
A, B, and C. 1975-1976.

maximum recorded at station C. In 1976, small pulses were noted in late April and early May at both stations A and C. Vertical distribution was uniform.

Synchaeta oblonga was usually found in water below 12°C. Ruttner-Kolisko (1974) stated it is usually found in the 12°C to 15°C range, but noted that some specimens from Iceland were found in colder water. Pejler (1957b) found it during winter and spring.

In my study S. oblonga was found while concentrations of edible phytoplankton were high. However, the importance of these cells as a limiting factor is questionable as the maxima in the main basin during September and October were much larger than the maximum at station C, despite higher concentrations of edible cells at station C. Cryptomonas was also higher at station C than at station A during September and October.

Synchaeta oblonga appeared able to tolerate moderately low oxygen concentrations. The population at station A during April 1976 was found in water that was 50% saturated. During the rapid population growth in September 1975, oxygen saturation was 80 to 100%.

Autumn populations of S. oblonga were associated with large populations of Keratella species. Small populations in spring were associated with high numbers of copepod nauplii and Polyarthra dolichoptera. Rapid increase in numbers of S. oblonga during fall 1975 occurred when the predator population was very low.

Polyarthra dolichoptera Idelson

Polyarthra dolichoptera has a very large virgate mastax.

De Beauchamp (1938 in Pejler, 1957a) found that, unlike many other
rotifers, Polyarthra would not accept Chlorella as food. Dieffenbach
and Sachse (1911 in Pejler, 1957a) found that Polyarthra euryptera
fed on Cryptomonas ovata but refused other cells of the same size.
Pejler (1957a) found Polyarthra vulgaris in seasons and locations
where Cryptomonas was present. In his statistical study, Edmondson
(1965) found that all cells smaller than Cryptomonas were insignifi-
cant in affecting the birth rate of P. vulgaris. He noted that the
birth rate was high when Cryptomonas was abundant and that the birth
rate varied when Cryptomonas was rare, indicating that P. vulgaris
is not totally dependent on Cryptomonas. He did find, however,
that variation in birth rates were more strongly correlated with
abundance of Cryptomonas than with water temperature.

Population densities at stations A and B were dropping rapidly
during late May 1975 and numbers were very low in early June (Fig.
43). Population density at station C was already low when sampling
began. A small increase in numbers began in late June at all stations
and continued to a peak in density in early July. Numbers declined
sharply in late July, but the populations persisted until mid-August.
The populations reappeared in late September at all stations, but
remained at low densities until late January. Numbers increased in
January and February with a higher maximum at station A than at
station C. Both populations declined in late March and early April.
Very rapid growth occurred at both stations immediately after ice
break-up. A maximum of 1400/liter at station A and 630/liter at
station C was reached in early May. Populations declined sharply
after the maxima and were low by late May at station C and by early
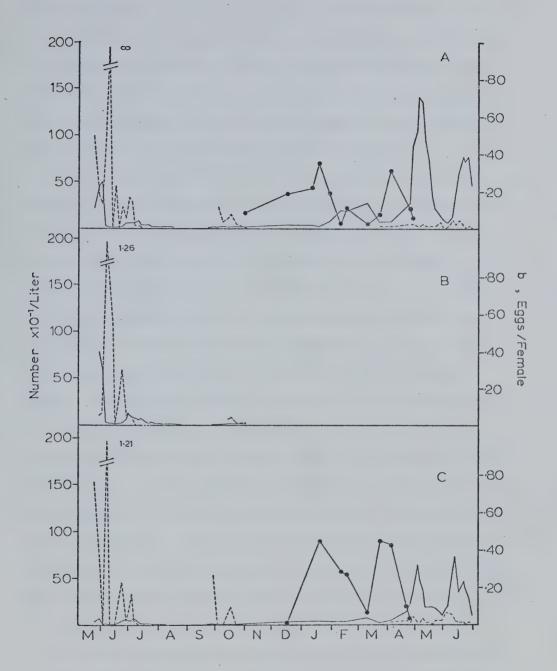
Figure 43. Population density, birth rate, and eggs per female
of <u>Polyarthra</u> <u>dolichoptera</u> at stations A, B, and C.
1975-1976.

———density

------birth rate

•——•eggs per female (winter only)

June at station A. Another period of rapid growth was seen in June. Numbers at station C reached a maximum of 700/liter in mid-June and the population at station A reached a maximum of 760/liter in the third week of June. Population densities declined immediately after the maxima and the numbers at station C were very low in late June while the population at station A was still declining.

During early June 1975 birth rates appeared very high, probably an artifact of small sample sizes. At all stations, a distinct pulse in birth rate was noted before the small population pulse in July and a pulse in birth rate was noted in October. During winter, increases in numbers were also preceded by increases in egg ratio. According to Amren's (1964a) data on egg duration, the birth rate would be very low at temperatures of approximately $1^{\circ}C$, but many of the eggs must have developed to produce the pulse in population density. The egg ratio dropped during the increase in density but rose again immediately after the pulse. The major increase in numbers, immediately after break-up, appears to be the result of this pulse in eggs. As with the winter population, the calculated birth rates appear to be erroneous as the increased egg ratio apparently caused the pulse in density. Increase in numbers during June was preceded by a very small increase in birth rate; birth rates in this case were low due to a low egg ratio and not due to low temperatures.

Amictic eggs were found in late May 1975 at stations A and C. No more amictic eggs were found until late April 1976 when they were again recorded at both stations. Numbers of amictic eggs rose to a maximum of 73/liter on May 7, 1976 at station A and 21/liter at station C on May 4, 1976. None were found at either station
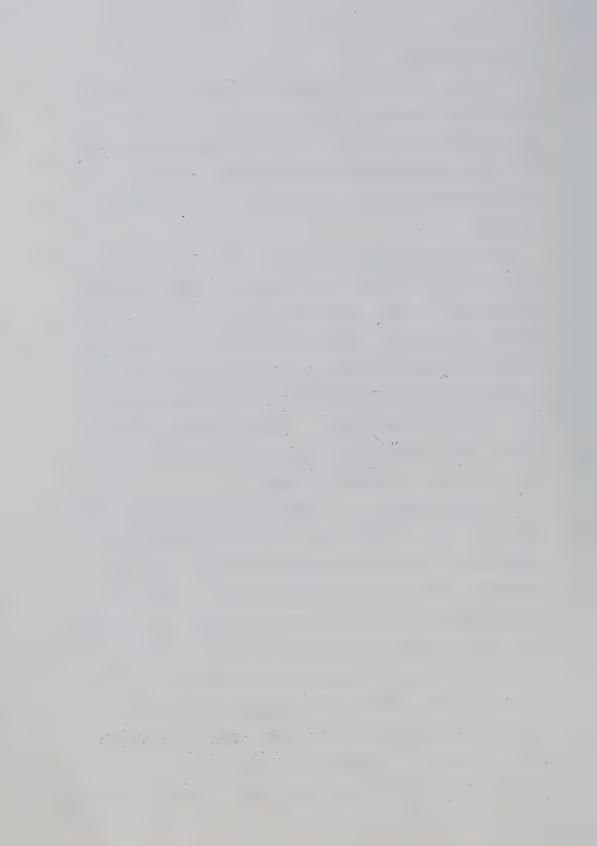
after May 14, 1976.

Vertical distribution of P. dolichoptera was uniform for much of the year. In July 1975 they avoided deep water that was less than 10% saturated with oxygen. A similar avoidance of low oxygen concentration was seen under the ice (Fig. 44). During the two pulses in spring and early summer 1976, the vertical distribution was uniform.

Polyarthra dolichoptera was found in temperatures from 0^oC to to 24.5^oC. The large maxima were found in cool water but the July pulse occurred in water temperatures averaging 20^oC. Amren (1964a) found highest numbers at temperatures of 10^oC and noted high birth rates at temperatures of 5^oC. Pejler (1957b) reports finding it during winter in eutrophic lakes and also in the hypolimnion of deep lakes during summer months. He notes in another publication (Pejler, 1961), however, that he has found it in water as warm as 19^oC and at depths of only 3 to 4 metres.

Polyarthra dolichoptera was present when the edible cell concentration was high. The small pulse in July 1975 declined as the concentration of edible cells dropped in mid-July. It would be premature, however, to single out concentration of edible cells as a limiting factor since, in spring 1976, numbers of P. dolichoptera were higher at station A than at station C despite more edible cells at station C. Decline in numbers during spring 1975 was accompanied by a drop in the concentration of Cryptomonas. The small pulse in July 1975 was accompanied by a very small pulse of Cryptomonas. However, increases of P. dolichoptera during winter were associated with low concentrations of Cryptomonas. Concentrations of Cryptomonas
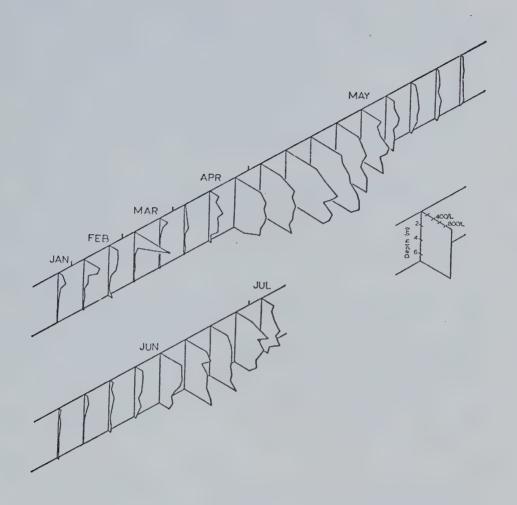
Figure 44. Vertical distribution of Polyarthra dolichoptera at station A. January 13-July 2, 1976.

were high during the early spring, 1976 pulse of P. dolichoptera at station C, but the spring pulse at station A occurred despite low concentrations of Cryptomonas. Thus in my study, the relationship between P. dolichoptera and Cryptomonas does not seem as clear as in studies with other species described earlier.

Polyarthra dolichoptera avoided areas of low oxygen concentration, but appeared to do well during winter despite saturation levels of only 20 to 40%.

When numbers of P. dolichoptera increased in early spring there were few animals present other than cyclopoid nauplii. Increases in July 1975 and June 1976 were associated with high densities of Keratella.

The pulse of P. dolichoptera at both stations during March 1976 occurred when predator populations were relatively low, but the late April and May pulse occurred while predators were common. Predator populations were still high but declining during the June 1976 pulse of this rotifer.

Trichocerca multicrinis Kellicott

Judging from the lack of information concerning T. multicrinis in the literature, it appears that this species is rare or absent in many parts of the world or, more likely, it is not considered truly planktonic. It is defined as planktonic, however, by Chengalath, Fernando, and George (1971).

Trichocerca multicrinis possesses a virgate mastax. Pourriot (1970 in Ruttner-Kolisko, 1974) reports that many species of Trichocerca pierce and suck the contents of algal cells and rotifer eggs.

Trichocerca multicrinis is a summer species in Hasting Lake.
Specimens were first collected from stations A and B in mid-June
(Fig. 45). Numbers increased during July to peak in late July and
early August, then declined sharply and rose again during mid-August.
Although the average population densities were comparable at stations
A and B, the peaks were more pronounced at station A. Numbers
declined slowly from late August through October. A few males were
found in late September at station A. No specimens were found under
the ice. In late May and June 1976 a few specimens were found
at station A.

Trichocerca multicrinis appeared later at station C than it did
in the main basin. The population density increased slowly through
July until a maximum was reached in the second week of August. This
peak coincided with the second major peak seen in the main basin,
but the density at station C was lower. Numbers declined slowly and
a few animals were still present in late October but none were found
under the ice. In 1976 T. multicrinis was found during late May and
June.

Vertical distribution was uniform throughout the year except
in early July when T. multicrinis avoided deep water which was low in
oxygen.

Although T. multicrinis was found in water as cold as $2^{o}C$, it
appeared to be most successful in warm water in Hastings Lake.
Major increases in population growth occurred in water above $20^{o}C$,
while the population declined at temperatures below $18^{o}C$. However,
the 1976 spring population started growing in water at $13^{o}C$. This
small pulse probably represented the hatching of resting eggs.
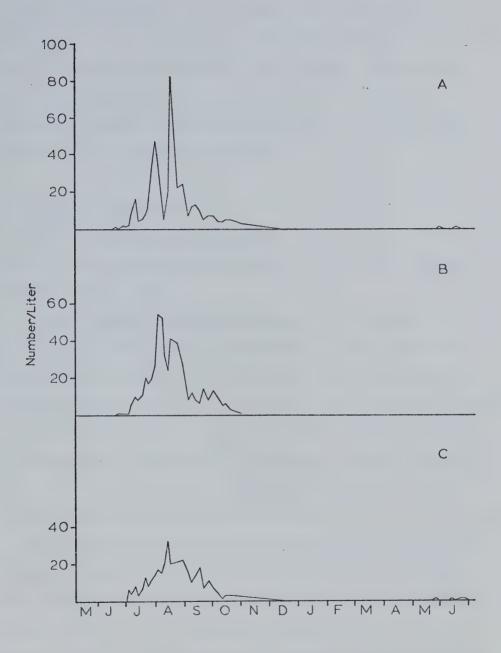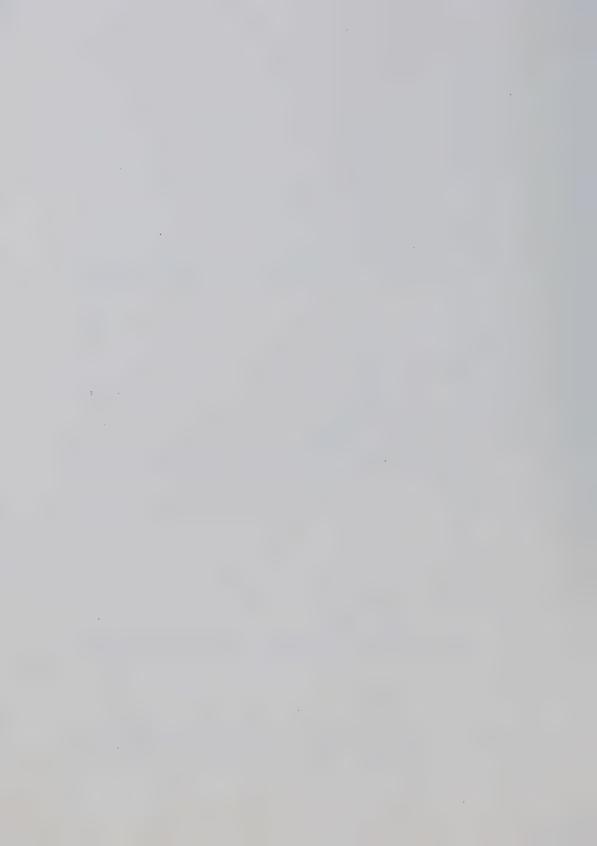
Figure 45. Population density of Trichocerca multicrinis at stations A, B, and C. 1975-1976.

Trichocerca multicrinis usually occurred when the water was well-oxygenated. As mentioned earlier, individuals appeared to avoid areas of low oxygen concentration during July 1975. This species was common during the crustacean dominance of the zooplankton community. Predator populations were relatively high during summer 1975 when T. multicrinis was most common.

Trichocerca stylata (Gosse)

Like T. multicrinis, T. stylata has a virgate mastax. It is small compared to T. multicrinis, being only 70 to 110 μ in length (Ruttner-Kolisko, 1974).

During my study, T. stylata was always rare. In the main basin a few specimens were found during July and one specimen was found in early October but none were found under the ice nor during spring and early summer 1976. At station C, a small population appeared in late July that developed to a maximum of 10/liter in early August. By mid-August, the population had disappeared. In 1976, specimens were found in late June and it appeared that the population was increasing when the study ended in early July.

Trichocerca stylata showed no preference for any particular depth during the study. It was usually found in water with temperatures over 15°C but an exception occurred in October when the temperature was approximately 10°C. Trichocerca stylata appeared in greatest numbers during the summer months when the phytoplankton was dominated by blue-green algae and the zooplankton was dominated by crustaceans. Oxygen concentrations were usually high when and where T. stylata

was found. The population at station A during July 1975 was
associated with relatively high numbers of predators.

Brachionus angularis Gosse

Brachionus angularis possesses a large malleate mastax with
five large, stout teeth on the uncus. The species is not known to
be a selective feeder, apparently feeding on algae and detritus
of suitable size (Ruttner-Kolisko, 1974). An important fact concerning
feeding of B. angularis was discovered during my study. During
observations of living B. angularis I noted that a few individuals
had filaments of Oscillatoria protruding from the mouth. The mastax
was observed to be pounding rapidly on the end of the filament.
These were not accidental occurrences as the animals were observed
"searching" for the end of the filament. When an individual
struck a filament it immediately stopped its normal spiralling motion,
then moved slowly along the edge of the filament until the end was
reached and maneuvered into the mouth. On most encounters the rotifer
failed to reach the end of the filament either because currents
moved the filaments away or else the rotifer apparently "gave up".
However, several successful attempts were noted and when the filament
was secure in the mouth the rotifer resumed its normal spiralling
action. It is apparent, therefore, that B. angularis, and possibly
other rotifers, can use some blue-green algae and perhaps some
other filamentous algae as food sources.

Brachionus angularis was rare in the main basin of Hastings Lake.
Specimens were first found in early June (Fig. 46). Numbers
remained low until early August when a small but distinct increase
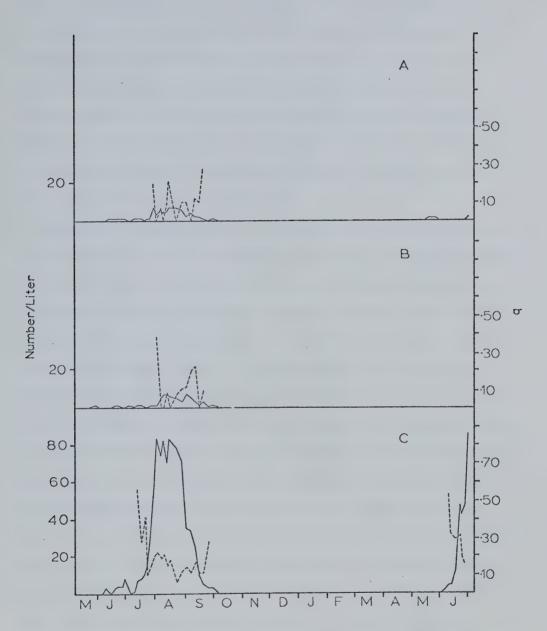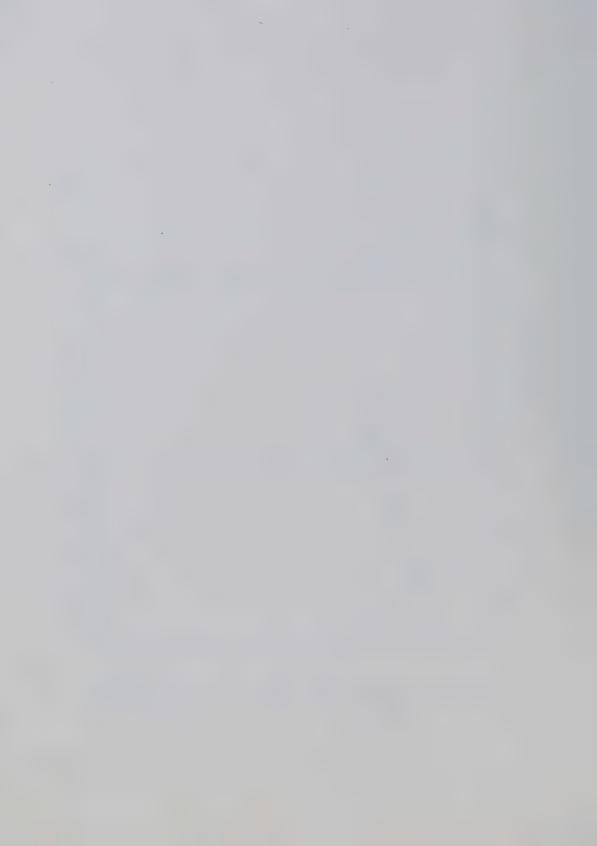
Figure 46. Population density and birth rate of <u>Brachionus</u>
<u>angularis</u> at stations A, B, and C. 1975-1976.

——— density

----- birth rate

was noted. Population density remained stable during August but a definite decline occurred in September until by mid-October the population had disappeared. A few animals were collected in early May, 1976, but the population disappeared and no more specimens were found until early July. During the small pulses at stations A and B, birth rates varied considerably. It is difficult to determine whether this reflects the actual birth rate or is the consequence of small sample sizes

Brachionus angularis occurred at station C at approximately the same time as it occurred at stations A and B, but the population density at station C was much greater than in the main basin. The population at station C remained small during June and early July, but a rapid increase was recorded in Mid-July. As numbers rose in July, birth rates dropped sharply from 0.56 eggs/female/day to a minimum of 0.10 eggs/female/day. In August, the population density levelled off and remained high for approximately four weeks. As soon as the density levelled off the birth rate rose to approximately 0.20 eggs/female/day and remained at 0.15 eggs/female/day until August 25 when it declined to 0.06 eggs/female/day. This drop in birth rate preceded a rapid drop in numbers through September until mid-October when no individuals were found. It appeared that the birth rate rose during the decline in numbers but again, sample sizes were small. In 1976 specimens were first found in early June at station C. Numbers increased suddenly and were still increasing on July 2. During this increase the birth rate dropped, in a manner almost identical to the 1975 population. An interesting situation arose during 1975 and 1976 when the populations were increasing. During mid-July 1975 a slight
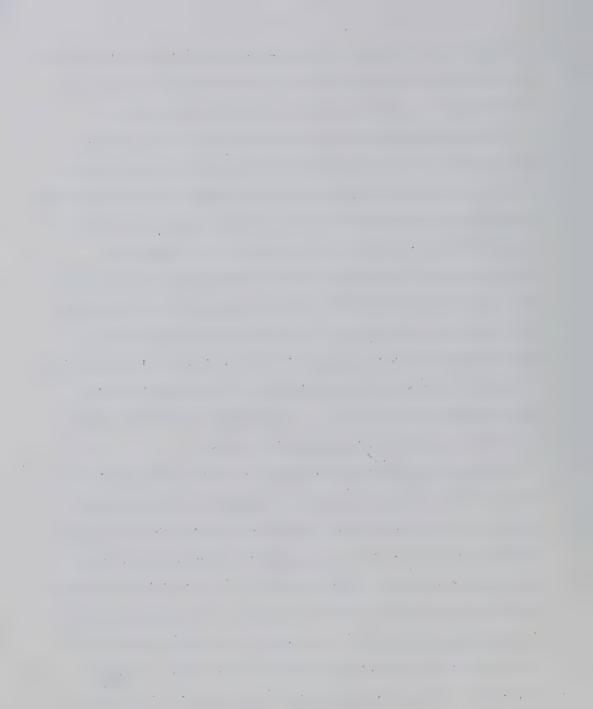
reduction in rate of population growth was accompanied by an increase in birth rate. In late June 1976, a slight decline in density was accompanied by a small but distinct increase in birth rate.

Brachionus angularis showed no preference for any particular stratum of water (Fig. 38). It was found in water between 12 and 24°C. In 1975 the population at station C remained low until the water temperature was nearly 20°C, while in 1976 the population increased rapidly in water at 14 to 16°C. Ruttner-Kolisko (1974) calls B. angularis a "eurythermous" species, but the absence of this animal at temperatures below 10°C and the long duration time of eggs below 10°C suggests it is restricted to warm water in Hastings Lake. Allan (1920) found B. angularis to prefer temperatures around 20°C and Chandler (1940) found it between 21 and 26°C while Arora (1966) found it between 21 and 35°C. The correlation coefficient between temperature and birth rate was 0.46 ($P < 0.05$).

Brachionus angularis appeared during the blue-green algal blooms. Allan (1920) found that it preferred "organically enriched areas" and Arora (1966) found maximum population densities in sewage ponds. Chandler (1940) also found B. angularis in association with blue-green algae and Pejler (1957b) describes it as a "eutrophic" species. These findings, coupled with my observations of B. angularis feeding on Oscillatoria, indicate the importance of blue-green algae to this species. I noted that rapid increase in numbers of B. angularis began while the Aphanizomenon-Oscillatoria group rose from "present" to "common". However, the population of B. angularis at station C declined in September, well before the major decline in Aphanizomenon-Oscillatoria.

Brachionus angularis was found in waters well-supplied with oxygen. The few specimens found during early July 1975 at station A were near the surface in well-oxygenated waters.
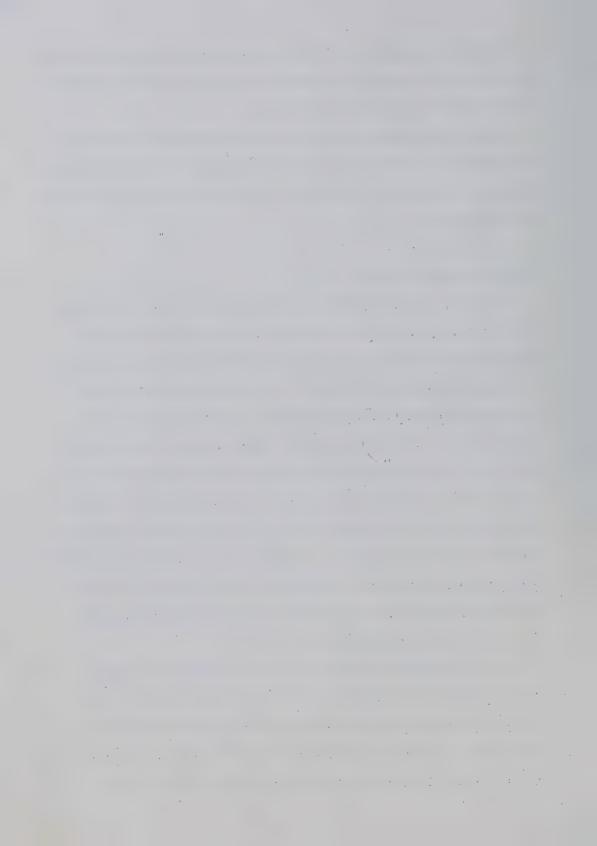
Brachionus angularis was common while the zooplankton community was dominated by crustaceans such as Diaptomus nauplii and copepodites, Bosmina, and Chydorus. At station A it was most common when predators were numerous.

Notholca squamula (Muller)

Notholca squamula possesses a small malleate mastax. Beauchamp (1938 in Pejler, 1957a) reported that it eats the small cells of Chlorella, but he could not maintain population growth on this diet.

Notholca squamula was always rare in Hastings Lake with small populations in spring and early winter. In late May 1975 a few animals were collected from station C while none were found in the main basin. In mid-December 1975, 1/liter were found at station A while 10/liter were found at station C. The population at station C had disappeared by mid-January 1976, but the population at station A persisted until late January. The 1976 spring population at station A first appeared in mid-May. Population density remained at 1/liter until early June when the population apparently disappeared, but two animals were found on July 2.

The 1976 spring population at station C appeared at roughly the same time as the station A population. Numbers remained low until an increase was noted in late May from 1/liter on May 28 to 13/liter on June 7. Immediately after this maximum the population declined and no specimens were found after June 11.

Notholca squamula appears to be a cold water species; it was found
in water from 1°C to 15°C, while population increases were seen in
temperatures as low as 2°C. These results concur with information
published on temperature ranges and geographic locations of N. squamula.
Amren (1964c) found N. squamula in arctic ponds and Pejler (1957a)
noted its presence during summer in ponds above the tree line.
Pejler (1957b) also found it in summer in lakes below the tree line
but noted it was only present in the hypolimnion.

With the exception of the early July 1976 recording, N. squamula
was present during times of high concentrations of the edible cells.
It was normally found in well-oxygenated water but appeared able
to withstand low oxygen concentrations since it was found during
January 1976 when the oxygen concentration was 30 to 40%.
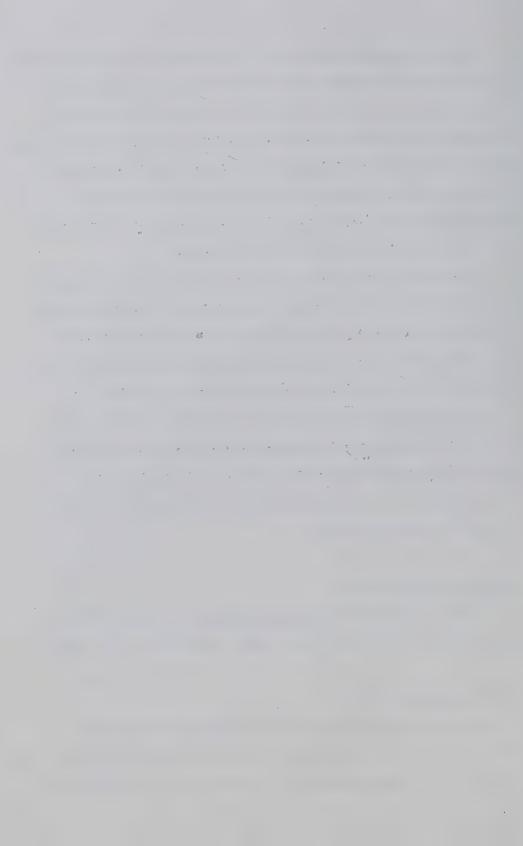
Notholca squamula was present with cyclopoid copepodites and
nauplii. It appeared with Polyarthra dolichoptera and was present
while the Keratella species were increasing during spring. The
1976 spring and early summer populations of N. squamula were assoc-
iated with numerous predators.

Keratella hiemalis Carlin

A single specimen of Keratella hiemalis was found on March 12,
1976 in water at 1°C and with an oxygen concentration of 5 to 10%.

Keratella quadrata Muller
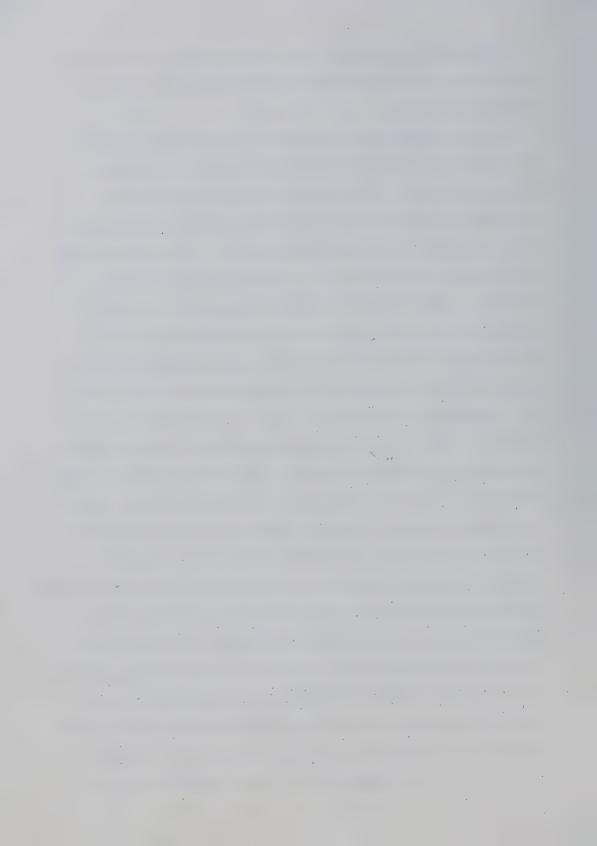
Keratella quadrata was one of the most common rotifers in
Hastings Lake during the study period. It is a very conspicuous
animal in the plankton, attaining lengths over 150 μ and possessing

two caudal spines. Nothing is known of its feeding habits, but its malleate mastax probably equips it to grind small phytoplankton cells and detritus.

Keratella quadrata was most abundant during spring and fall and it showed the same basic pattern of occurrence at all three stations (Fig. 47). Numbers in the main basin population were increasing when sampling began in late May. Population densities rose to a maximum in the second week of June. Birth rates were high during late May and early June, but dropped as the population increased. After the maxima, numbers at both stations dropped rapidly but rose again during late June and stabilized somewhat until mid-July. Birth rates rose during and immediately after the major decrease in density. While populations were stable in early July the birth rate was stable at station A, but appeared to rise at station B. After mid-July, the numbers declined at both stations and continued dropping until August when a slight peak was noted. During the decline in July and early August, the birth rate peaked twice, once when the population declined sharply in the third week of July and once in early August, immediately before the small peak in population density. The density remained low during August and through the first half of September. Birth rates were relatively high during this period but fluctuated at station B. Numbers began to increase in mid-September and continued increasing, reaching a maximum in late October. Birth rates remained relatively high during the early fall increase in numbers, but started to decline during October and were low by late October when population growth had stopped.

Despite low birth rates in late fall the population density
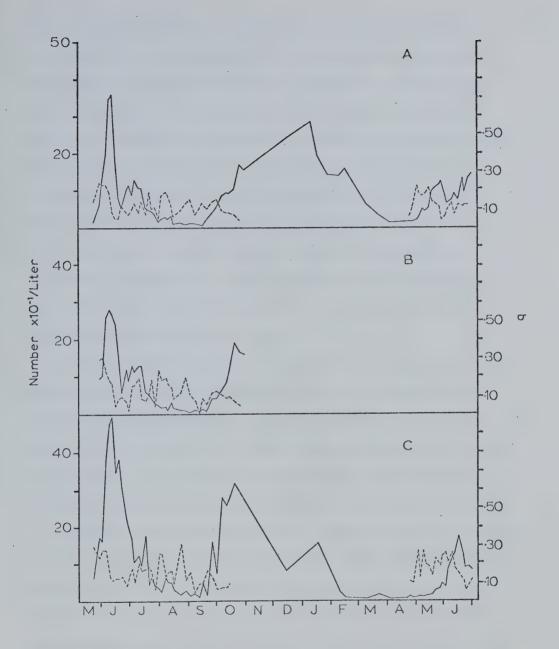
Figure 47. Population density and birth rate of <u>Keratella</u> <u>quadrata</u>
at stations A, B, and C. 1975-1976.

——————density

------birth rate

of K. quadrata at station A increased during December and January.
In December, 27% of the animals carried an egg, but egg duration
data (Fig. 34) indicated that duration times were extremely long,
thus resulting in low birth rates. In mid-January, the density
declined but appeared to stabilize in mid-February. After February
the density dropped again and numbers were very low in April.
Population density rose slowly to a maximum in late May 1976, but
was much lower than the 1975 maximum. Birth rates were very high
during late April and early May, but dropped as the population
increased. In early June a drop in density was associated with a
pulse in the birth rate, followed by an irregularly increasing
density during the remainder of June.

Population growth at station C was similar to the growth in the
main basin. The initial increase in numbers during late May and
early June was accompanied by a decrease in birth rate, while a
slight decrease in numbers on June 2, 1975 was accompanied by a pulse
in birth rate. The population density reached a maximum in the
third week of June while the birth rate was low. Numbers at station
C at this time were higher than those at stations A and B, but dropped
during the remainder of June and early July. This period of decline
lasted longer than the corresponding decline in the main basin.
Like the main basin, a secondary pulse occurred in the north-east
basin during July, followed by a decline during late July and early
August. The minimum in early August was accompanied by a peak in
birth rates. A slight peak in density occurred during mid-August,
followed by a gradual decline to a minimum in mid-September.
Birth rates appeared similar to those in the main basin with a

peak in late August and then a decline to a minimum in early
September. Numbers increased in an irregular fashion during late
September and October and stabilized somewhat during mid-October.
Birth rates climbed during the second and third week of September,
but declined in late September and early October. During early winter,
numbers dropped quickly at station C. An increase was noted during
January but by mid-February numbers were very low and remained low
until May 1976. Population density of K. quadrata increased very
slowly during late May; major increases were not seen until June.
During this period the birth rate fluctuated but remained high.
The first major drop occurred in June when the population showed
a major increase to a peak in mid-June, followed by a decline during
late June and early July. The 1976 peak at station C was similar
in timing but much smaller than the peak in 1975. Also, the 1976
peak at station C was similar in size to that at station A but occurred
almost a month later.

Keratella quadrata showed a uniform depth distribution for most
of the year (Fig. 48). During July 1975, it appeared to prefer the
warm surface waters that were supersaturated with oxygen. In mid-
December the population concentrated in deeper water but as winter
progressed and oxygen was depleted at lower depths the population
moved to surface waters.

Keratella quadrata was found throughout the year in temperatures
of $0^{\circ}C$ to $24.5^{\circ}C$. Populations increased in both warm water (above
$20^{\circ}C$) and cold (below $5^{\circ}C$) although the birth rate was always low
below $5^{\circ}C$. High population densities were maintained during the
winter despite temperatures of 0 to $2^{\circ}C$. Allan (1920) found
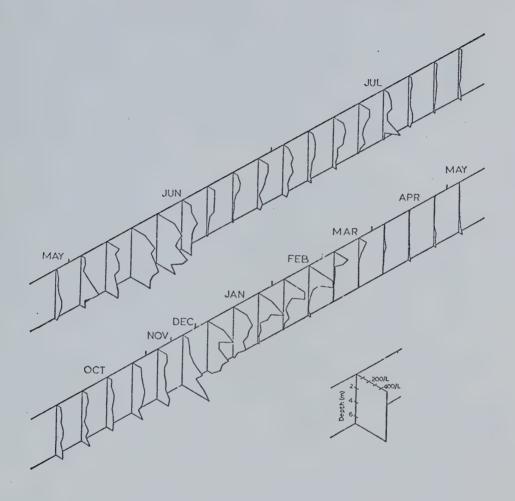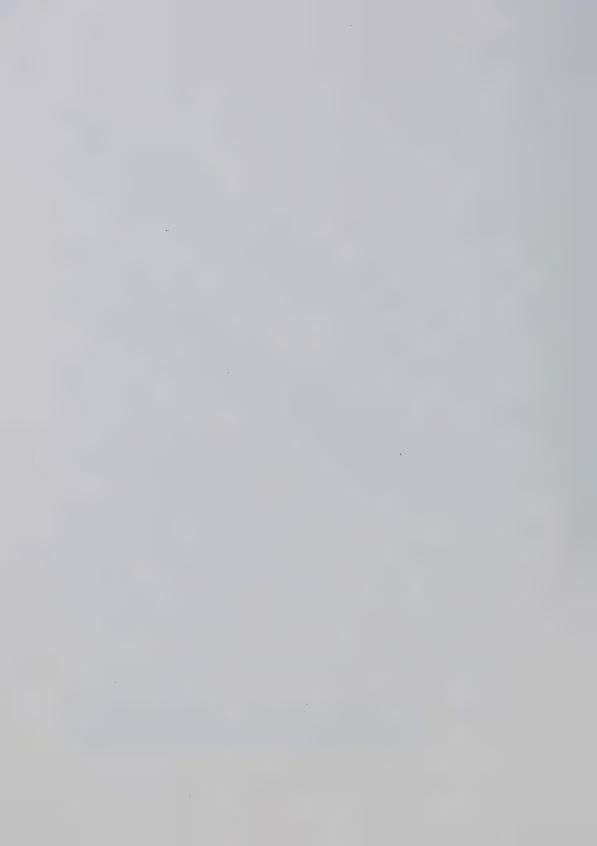
Figure 48. Vertical distribution of _Keratella quadrata_ at station A. May 30-July 25, 1975; October 13, 1975-May 4, 1976.

K. quadrata common up to 23°C and noted increases during January
and June. Amren (1964a) found that his Spitzbergen populations
increased rapidly above 5°C and Davis (1954) found this species
most common betwwen 4°C and 10°C. Ahlstrom (1943) found specimens
in the hypolimnion of Lake Michigan during the warm months. George
and Fernando (1969) found that numbers of K. quadrata increased
during the winter at all depths, while during summer it was only
found in the hypolimnion.

Keratella quadrata populations usually increased when the
phytoplankton community was rich in edible cells, but small increases
were noted during July when blue-green algae were dominant. Allan
(1920) found K. quadrata more common near sewage outlets and Chandler
(1940) found it most common when members of the Chlorophyceae were
present. Amren (1964a) found marked reductions in birth rate of
K. quadrata that did not coincide with changes in the "small monad"
populations. He suggested that changes in age structure of the
population and changes in fecundity of generations could be responsible
for changes in birth rate.

Figure 49 shows the relationship between birth rate and temper-
ature. The border, delineating the left side of the graph from the
right side, probably represents maximum possible birth rate under
the temperature conditions. The correlation coefficient between
birth rate and temperature is 0.56 ($P < 0.01$). The fact that the
highest birth rate was recorded when the water temperature was 14°C
and that the border on the graph slopes downward at temperatures
above 15°C may indicate a temperature inhibition of birth rate
above 15°C. It is also possible, however, that the decline in
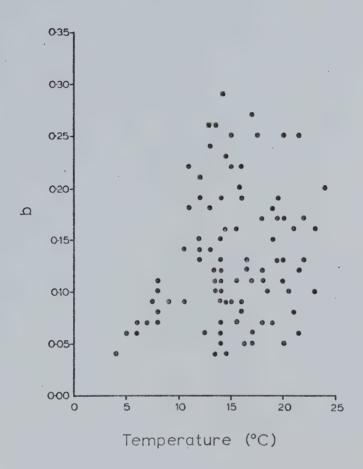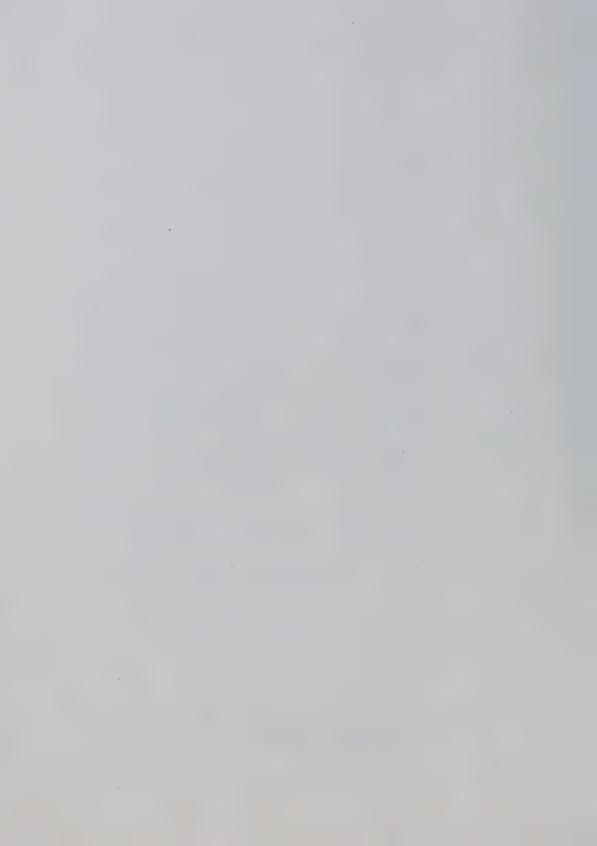
Figure 49. Relationship between temperature and birth rate of _Keratella_ _quadrata._

birth rate above 15°C was partly due to reduction in concentration
of the total edible cells during summer.

The relationship between birth rate and concentration of
edible cells is more obscure than that between birth rate and tempera-
ture. The correlation coefficient between birth rate and concentrarion
of edible cells is 0.10 (N.S.) when data for the entire year are used
If points from the ice-free period only are used, the correlation
coefficient is 0.48 (P < 0.01). This discrepancy is a result of
winter water temperatures. Amren (1964a) showed that at 1°C,
typical of the ice-covered period, the development time of
K. quadrata eggs would be extremely long; thus the birth rates would
be low despite high edible cell counts.
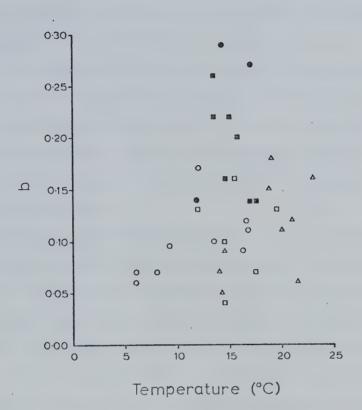
Despite these positive relationships between temperature and birth
rate and between birth rate and edible cell concentrations, interpreta-
tion of Figure 50 still poses a few problems. As expected the border
is lined with points of high edible cell concentrations, but a
number of points of high edible cell concentrations are found well
below and to the right of the border. In other words a high concen-
tration of edible cells and a suitable temperature are not always
associated with a relatively high birth rate.

Keratella quadrata was found in a wide range of oxygen satura-
tions. During calm weather in July 1975 and during winter, the
majority of the population moved from poorly-oxygenated waters
near the bottom to surface waters. Despite this apparent preference
for well-oxygenated waters, K. quadrata survived during the winter
when oxygen saturation was low. For example, during March 1976
animals were found in water less than 10% saturated with oxygen.

Figure 50. Relationship between temperature, total edible cells,
and birth rate of Keratella quadrata.

● >10,000 cells/ml

▪ 5,000-10,000 cells/ml

○ 2,500-5,000 cells/ml

□ 1,000-2,500 cells/ml

△ <1,000 cells/ml

Temperature (°C)

Keratella quadrata was common in Hastings Lake when the zooplankton community was dominated by the congeneric species K. cochlearis and and K. earlinae. In 1975, the first major peak of K. quadrata preceded that of the other two Keratella species, while the secondary peaks of K. quadrata coincided with the first peaks of K. cochlearis and K. earlinae. During fall 1975, K. quadrata increased at the same time as K. cochlearis while K. earlinae started increasing more than a week earlier. In spring 1976, K. quadrata increased at the same time as K. cochlearis. Copepod nauplii were often abundant immediately before and after K. quadrata peaks; Daphnia pulicaria persisted at high population densities while populations of K. quadrata declined in early summer.

Keratella quadrata showed rapid population growth in late May and early June 1975 while predator density was low. The population declined in June as predators increased and the density was low during July and August when predators were common. The fall increase in numbers of K. quadrata occurred as the predator population declined. During May and June 1976, the population growth rate of K. quadrata was low when Cyclops bicuspidatus thomasi was abundant. The correlation coeffecient between density of K. quadrata and density of predators was -0.22 (N.S.) (Table 5).

Average lorica and spine lengths of K. quadrata are shown in Figure 51. During late May and June 1975, when the water was warming rapidly and the population was growing, lorica length at both stations was decreasing while spine length was increasing. In July, spine length decreased suddenly and lorica length continued to decrease.

TABLE 5

Correlation coefficients between rotifer density, spine length and lorica length, and cyclopoid copepods. "Predators" represents the summation of the density of <u>Cyclops bicuspidatus thomasi</u> IV - VI and <u>Cyclops vernalis</u> IV - VI.

		Copepodites I - III	Cyclops bicuspidatus thomasi IV - VI	Cyclops vernalis IV - VI	Predators
<u>Keratella</u> <u>quadrata</u>	Spine Length	-0.20 (N.S.)	-0.35 (N.S.)	-0.50 (N.S.)	-0.68 (P < 0.05)
	Lorica Length	0.260 (N.S.)	-0.09 (N.S.)	-0.84 (P < 0.01)	-0.55 (N.S.)
	Density	0.008 (N.S.)	-0.01 (N.S.)	-0.44 (N.S.)	-0.22 (N.S.)
<u>Keratella</u> <u>earlinae</u>	Spine Length	0.001 (N.S.)	0.54 (N.S.)	0.30 (N.S.)	0.63 (P < 0.05)
	Lorica Length	0.01 (N.S.)	-0.55 (N.S.)	-0.40 (N.S.)	-0.74 (P < 0.01)
	Density	0.14 (N.S.)	-0.68 (P < 0.01)	-0.02 (N.S.)	-0.65 (P < 0.05)
<u>Keratella</u> <u>cochlearis</u>	Spine Length	0.03 (N.S.)	0.74 (P < 0.01)	0.17 (N.S.)	0.46 (N.S.)
	Lorica Length	0.36 (N.S.)	-0.05 (N.S.)	-0.75 (P < 0.01)	0.22 (N.S.)
	Density	-0.06 (N.S.)	0.27 (N.S.)	-0.06 (N.S.)	0.24 (N.S.)
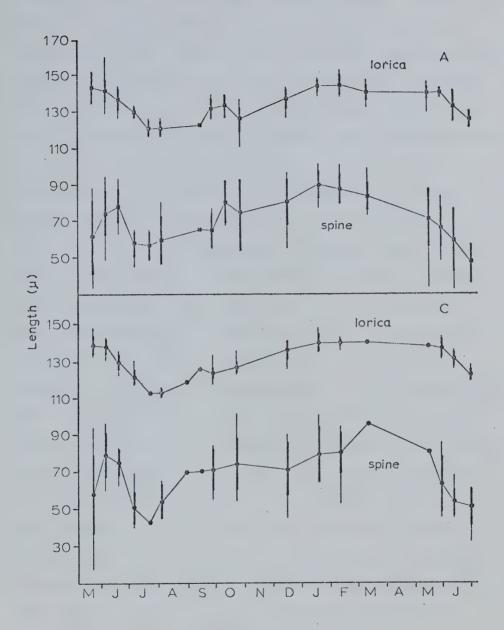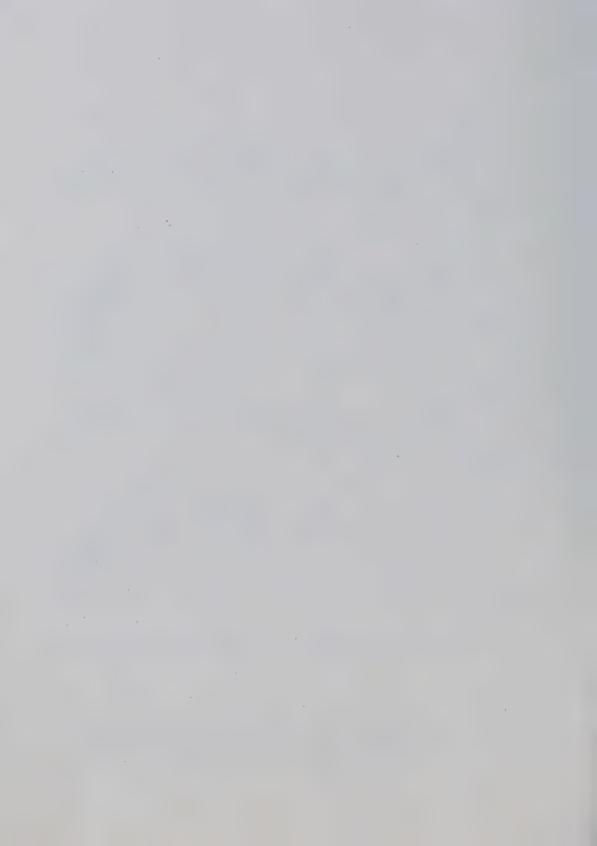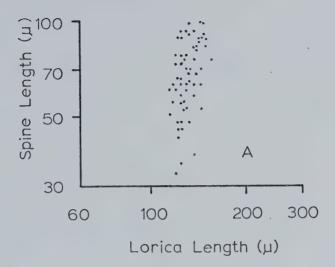
Figure 51. Average lorica and spine lengths of <u>Keratella quadrata</u> at stations A and C. 1975-1976. Thick bars indicate one standard deviation, thin bars indicate the range.

The sudden decrease in spine length occurred during the warmest time of the year and immediately after the maximum population density. During late July and August, while water temperatures were dropping and the population was low, both spine and lorica lengths increased with animals at station C showing larger increases than those at station A. During fall, lorica and spine lengths continued to increase. The graph for station A shows a sudden increase in both spine and lorica lengths during September, but both lengths appeared to decline again in late October. These increases in length occurred while the water temperature was dropping quickly and the population was growing. The population was stable when the lengths declined in October. During early winter both of these measurements increased slowly. The population at station C was declining during this period while the population at station A showed some increases. After February, the spine lengths at both stations declined while the lorica lengths remained constant. This decline in spine length continued through the spring and early summer of 1976. The lorica length remained constant through early spring but dropped during June. The water temperatures were increasing during May and early June but dropped in late June. The population showed slow growth during the period of declining spine and lorica lengths in spring 1976. The correlation coeffecient between temperature and spine length was -0.73 (P < .01), and the coeffecient between temperature and lorica length was -0.57 (P < .01).

Figure 52 shows the relationship between spine length and lorica length. The correlation coeffecient between the two lengths was 0.56 (P < .01) at station A and 0.48 (P < .01) at station C.
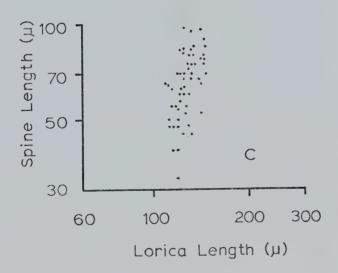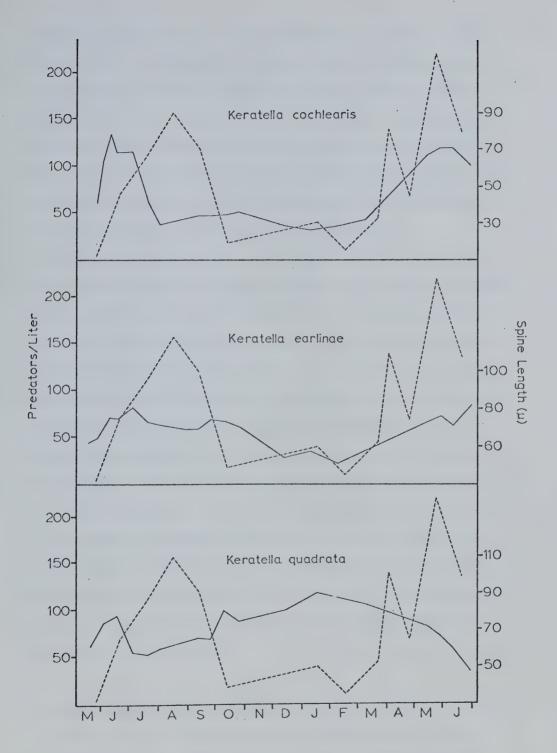
Figure 52. Relationship between lorica length and spine length of <u>Keratella</u> <u>quadrata</u> at stations A and C.

Figure 53. Spine length of <u>Keratella quadrata</u>, <u>K</u>. <u>cochlearis</u>,
and <u>K</u>. <u>earlinae</u> with density of predators. 1975-1976.

————spine length

------predator density

Despite general increases in spine length with increases in lorica length, there is a large range of spine lengths for any particular lorica length. A sign test (Sokal and Rohlf, 1969) was used to determine any difference in both spine and lorica length between stations A and C. Average lorica and spine lengths were computed from each measured sample from station A and compared to the corresponding sample from station C. No signifigant difference between stations was found in either spine or lorica length.

During early summer 1975, spine lengths increased and lorica lengths decreased as the predator population grew (Fig. 53). However, both lengths dropped in July when the predator population was still growing. A sudden increase was noted in both lengths as numbers of predators declined in October 1975. Both spine and lorica lengths were long in winter while predator populations were low. In spring 1976 spine lengths decreased as predator populations grew and lorica lengths dropped in June when predators were still numerous but declining. The correlation coeffecient between spine length and predator density was -0.68 ($P <$ .05) and the coeffecient between lorica length and predator density was -0.55 (N.S.), (Table 5). Neither spine nor lorica lengths were correlated with numbers of Cyclops bicuspidatus thomasi, but a signifigant ($P <$ .01) negative relationship occurred between the density of Cyclops vernalis and lorica length (Table 5).

Taxonomy of Keratella cochlearis and Keratella earlinae

Taxonomy of the "cochlearis group" (Ruttner-Kolisko, 1974), genus Keratella, is a difficult area of study. Ahlstrom (1943)

determined several species and numerous varieties in this group. Ruttner-Kolisko (1974) prefers to call the entire group Keratella cochlearis and describes three major series, noting that morphological varieties seen in each series are often associated with environmental factors. Two easily distinguished forms were found in Hastings Lake, one corresponding to Ruttner-Kolisko's tecta series, (Ahlstrom's K. cochlearis) and one to Ruttner-Kolisko's irregularis series (Ahlstrom's K. earlinae). In my study Ahlstrom's original classification is used for the following reasons. The two forms showed an obvious and consistent difference in dorsal sculpturing of the lorica (Fig. 54), a characteristic considered to be of great taxonomic importance (Ahlstrom, 1943). Keratella cochlearis possesses a mid-dorsal keel while K. earlinae possesses irregular facets. Keratella earlinae was consistently bigger than K. cochlearis and showed a less exhuberant form of cyclomorphosis, although timing of major cyclo-morphic events were similar. Birth rates of K. cochlearis were almost always higher than those of K. earlinae. When specimens were observed swimming, the rate of spiralling was clearly faster in K. cochlearis than in K. earlinae. The two forms also showed differences in vertical distribution during the calm period in July 1975. Keratella cochlearis concentrated in surface waters while K. earlinae preferred deeper water. Although criteria such as these may not warrant separating two forms into species, the forms seemed distinctive enough to warrant separate consideration of their populations.

Keratella cochlearis

Keratella earlinae

Figure 54. Dorsal views of Keratella cochlearis and K. earlinae
to show sculpturing. (After Ahlstrom, 1943.)

Keratella cochlearis (Gosse)

Keratella cochlearis has a relatively large malleate mastax.
Naumann (1923 in Pejler, 1957a) noted that it shows little preference
in selecting food particles. His experiments showed that specimens
would fill their guts with carmine particles. Luntz (1926 in Pejler,
1957a) maintained a population of K. cochlearis on the flagellate
Polytoma, and de Beauchamp (1938 in Pejler, 1957a) showed that K.
cochlearis could eat Chlorella, but his populations died after one
generation. Pejler (1957a) noted that K. cochlearis eats particles
below 10-12 μ in diameter.
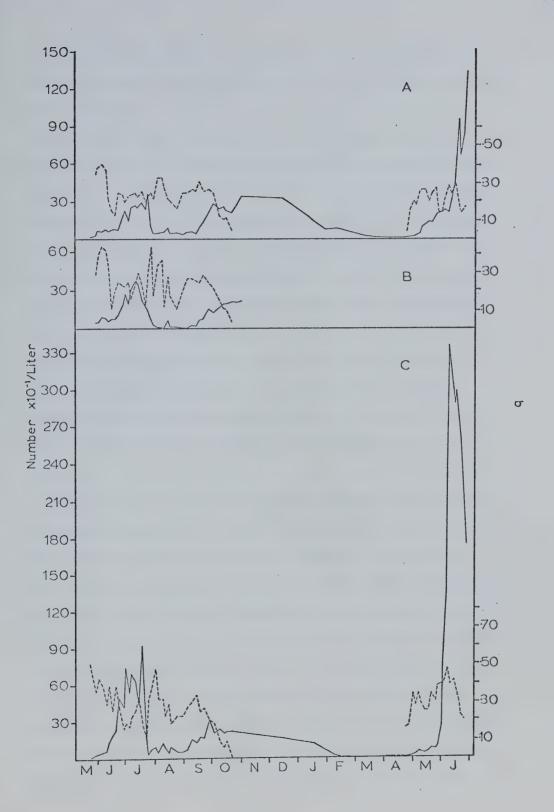
Like K. quadrata, K. cochlearis was most common during early
summer and fall (Fig. 55). Populations at stations A and B were very
low in late May 1975 and remained low with minor increases until
late June when they increased rapidly. Birth rates were high in
early June, but dropped rapidly in mid-June. A few days before the
rapid increase in density the birth rates rose again. After
increasing, the population appeared to level off and remained high
for most of July with stable birth rates for most of this period.
In late July, at both stations, a major decrease in density occurred,
leaving very low numbers in early August. Numbers remained low
until mid-August when a minor pulse was seen at both stations.
Birth rates increased as the population dropped, and remained high
during early August. A drop in birth rate occurred during the short
pulse in density. Population density dropped again after the August
pulse and remained low until mid-September and appeared to stabilize
during October. Birth rates climbed during late August and remained

Figure 55. Population density and birth rate of <u>Keratella</u> <u>cochlearis</u>
at stations A, B, and C. 1975-1976.

——— density

------ birth rate

high until early October when an obvious decline was observed. The egg ratio was high during October, but cold water temperatures caused low birth rates.

Winter was a period of slow decline in numbers. Numbers remained high during December but declined during January, February, and March to low densities in early April. Numbers increased slowly through May and early June, followed by a rapid increase in numbers during the second week in June. Numbers dropped during late June, but rose again immediately afterward and were still increasing in early July. Birth rates rose rapidly in late April and remained high for most of May, then dropped in early June, but rose again immediately before the period of rapid population increase. Birth rates dropped again when the population was increasing rapidly. Rate of population growth appeared much faster in 1976 than in 1975 and maximum population size was higher in 1976 than in 1975.

Seasonal occurrence of K. cochlearis at station C was similar to that in the main basin. The population showed a rapid increase that started in mid-June and rose to a maximum in early July. This increase occurred approximately two weeks earlier than increases at stations A and B. Birth rates dropped while the population was increasing, but the rate of decline was not as rapid as the decrease in birth rate seen in the main basin. Both numbers and birth rates levelled off for most of July although a drop in numbers during mid-July was accompanied by a pulse in birth rate and a subsequent pulse in density. The population dropped rapidly in late July and remained low, with minor peaks during August. Birth rates rose

immediately after the decline in density and were very high in early August, but dropped again during the next two weeks. Population density increased slowly during September and reached a maximum in late September. Numbers dropped slightly immediately after the maximum but appeared stable for the rest of October. Birth rates rose in mid-August when numbers were low. They continued to rise with the population in the first two weeks of September, but dropped during late September and was very low in late October. The winter population at station C was similar to that at station A. Numbers dropped rapidly in January and February and remained very low during March and April. Population density increased slowly during May while birth rates were high. A very rapid increase in density was noted during early June, reaching a maximum on June 18. Numbers decreased immediately after the maximum and were still decreasing in early July. Birth rates remained high, even increasing slightly during the phase of rapid growth in early June, and did not drop until the population maximum was reached. The 1976 spring population increase at station C occurred earlier than the 1975 increase and earlier than the 1976 spring increase at station A.

Vertical distribution of K. cochlearis is shown in Figure 56. During spring and early summer, distribution was uniform, but in early July a preference for the surface was observed before the oxygen saturation declined in the deep water. As the calm period in July continued and oxygen was depleted near the bottom, the population moved away from the bottom layers. In December, concentrations were found near the surface and near the bottom. As the oxygen was depleted in
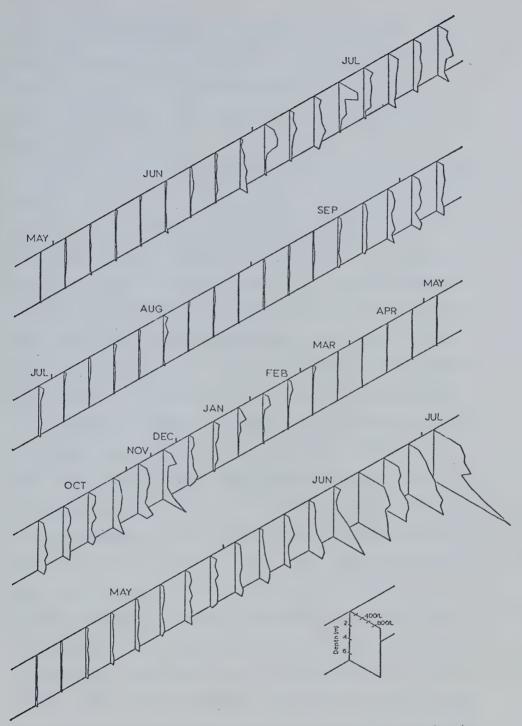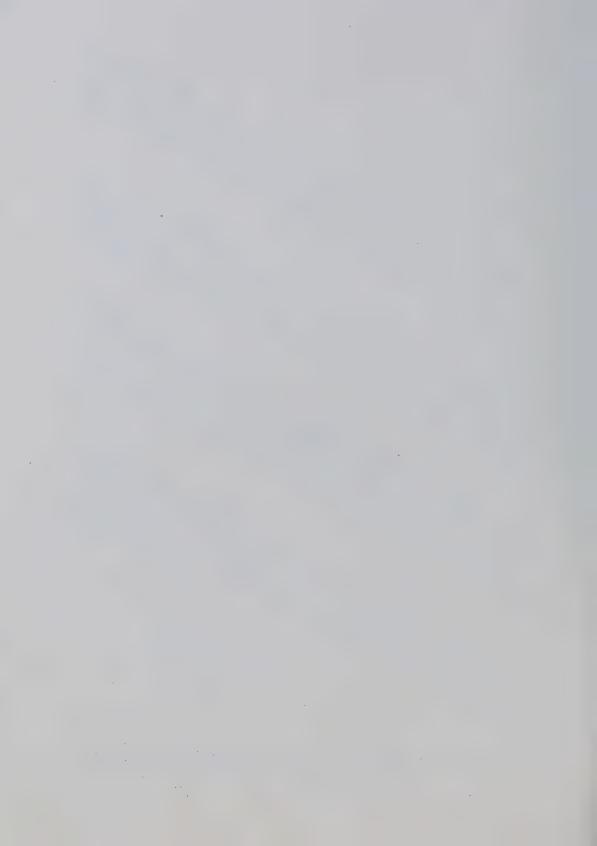
Figure 56. Vertical distribution of _Keratella cochlearis_ at station A. May 30, 1975-July 2, 1976.

lower depths the population concentrated in the top metre. The
spring 1976 population showed a uniform distribution pattern but
during late June and early July the majority of the animals
concentrated near the bottom, quite unlike the pattern seen in
early July 1975.

Keratella cochlearis was found in a wide range of temperatures
from $0^{\circ}C$ to $24.5^{\circ}C$. It was noted, however, that major increases in
density did not occur below $12^{\circ}C$ and that birth rates were low
below $10^{\circ}C$, an obvious result of long egg duration at temperatures
below $10^{\circ}C$. Numerous references exist in the literature concerning
the relationship between K. cochlearis and temperature. Many authors
report that maximum population densities occur in spring or early
summer and fall (Allen, 1920; Beach, 1960; Campbell, 1941; Chandler,
1940). Ahlstrom (1943) found maxima in summer in the hypolimnion
of Lake Michigan. Campbell (1941) and Chandler (1940) both noted
that spring maxima occurred in cooler water than fall maxima.
Davis (1954) found population maxima over $13^{\circ}C$ and noted that
K. cochlearis was rare under $5^{\circ}C$. George and Fernando (1969)
found K. cochlearis to be a "cold stenotherm" in Sunfish Lake,
Ontario with maxima in January, but in nearby Paradise Lake they
found maxima in June with small populations during winter.
Edmondson (1965) showed a strong relationship between birth rate
and temperature. The upper temperature limit of K. cochlearis
appears unknown. Edmondson's data show high birth rates at $20^{\circ}C$
and Arora (1966) found specimens at temperatures over $21^{\circ}C$. Horkan
(1971) found K. cochlearis eggs at temperatures as high as $26.6^{\circ}C$.

Major increases in population density of K. cochlearis occurred

while the edible cells were in relatively high concentrations. However, concentration of edible cells often dropped as numbers of K. cochlearis rose and maximum densities of K. cochlearis were often found with relatively low cell populations. The early summer population of K. cochlearis was stable during the dominance of the Cyanophyta. At station A, changes in the birth rate of K. cochlearis closely followed changes in the concentration of edible cells during spring and fall of 1975. However, high birth rates were noted in summer when the concentration of edible cells was low.

It is difficult to interpret literature concerning food resources and K. cochlearis as many early researchers collected phytoplankton samples with a net, thereby losing the small cells now realized to be important to rotifers. Allen (1920) found K. cochlearis was more plentiful in areas of high concentrations of organic matter. Both Chandler (1940) and Davis (1954) found K. cochlearis in association with spring diatom blooms and Chandler found numerous K. cochlearis during fall when blue-green algae were common. Davis found fall populations associated with green algae, but did not collect the small cells. Edmondson (1965) associated certain phytoplankton species with high birth rates. He found Chrysochromulina, Stichococcus and miscellaneous flagellates to be significantly correlated with birth rate. He reported that Rhodomonas was of minor importance while Cryptomonas, Chlamydomonas, and colourless flagellates did not signifigantly affect the birth rate. In another work (Edmondson, 1960) he found an increase in birth rates after fertilizing the lake. Increased birth rates were correlated with a large concentration of Ankistrodesmus.

Figure 57 shows the relationship between birth rate and
temperature. As with the similar graphs for Pompholyx sulcata
and Keratella quadrata, the border probably represents the maximum
birth rate possible under the temperatures indicated. It is important
to note that the border extends farther to the upper right side of
the graph than it does on the graph of K. quadrata. The second
highest birth rate occurred at a temperature of $22^{\circ}C$. It seems,
therefore, that the effect of temperature on the birth rate is linear
within the range found in Hastings Lake and that the birth rate was
not adversely affected by high temperatures. The correlation
coefficient of temperature and birth rate was 0.73 (P < .01).

Figure 58 shows the relationship between birth rate, temperature
and phytoplankton. The correlation between birth rate and the
concentration of phytoplankton cells measured during the ice-free
periods was 0.42 (P < .05). As expected, the border consists largely
of points of high edible cell concentrations and the right side of the
graph consists of points of low edible cell concentrations. Several
exceptions to this generalization are apparent, however. For example
it is noted that a dark square, indicating edible cell concentrations
of 5000/ml to 10,000/ml, is positioned well below the border, as are
two open squares representing phytoplankton concentrations of 1000/ml
to 2500/ml. Thus, as with K. quadrata, a high concentration of cells
is not always associated with a relatively high birth rate.

Since K. cochlearis was present during the entire sampling period,
it withstood a wide range of oxygen concentrations. During the calm
period in July 1975, animals avoided the depths that were less than
10% saturated. During early winter, many animals were found near
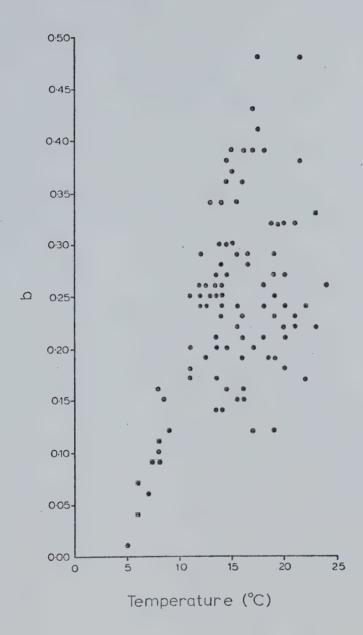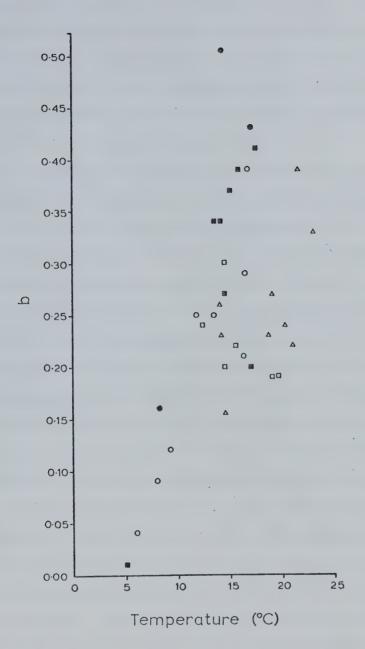
Figure 57. Relationship between temperature and birth rate of Keratella cochlearis.

Figure 58. Relationship between temperature, total edible cells,
and the birth rate of Keratella cochlearis.

    ●   > 10,000 cells/ml

    ▣   5,000-10,000 cells/ml

    ○   2,500-5,000 cells/ml

    □   1,000-2,500 cells/ml

    △   < 1,000 cells/ml

the bottom although the water was less than 20% saturated. As in July, however, the population avoided areas less than 10% saturated. Oxygen saturations at station C were below 10% for most of February and March 1976, and although K. cochlearis was present at this time, the population was much smaller than the main basin population where oxygen depletion was less severe.

Keratella cochlearis was dominant in early summer and fall along with K. quadrata and K. earlinae. It was noted, however, that K. quadrata sometimes peaked earlier than K. cochlearis. It was also noted that when K. earlinae was dominant in early summer 1975, K. cochlearis was relatively rare, while in summer 1976 when K. cochlearis was very abundant, K. earlinae was rare. Daphnia pulicaria populations were often dense when K. cochlearis was abundant but most of the other crustacean species were rare at these times. Elgmork (1964) found maximum K. cochlearis populations when cladoceran populations were low and suggested a competitive relationship between the two.

The major increase in density at station A during late June 1975 occurred while the density of predators was increasing. Predator population density was still increasing in July while numbers of K. cochlearis were stable, and low densities of K. cochlearis in August were correlated with a peak in predator density. The fall increase in K. cochlearis occurred as predators declined to low densities in October. Keratella cochlearis showed slow population growth, despite high birth rates, in May 1976 when numbers of Cyclops bicuspidatus thomasi were high. Rapid growth of the K. cochlearis population was seen in June when predators were still numerous but declining. The correlation coefficient between the density of K.

cochlearis and the density of predators was 0.24 (N.S.). The correlation coefficients between the density of K. cochlearis and the densities of the two predatory copepods, C. bicuspidatus thomasi and C. vernalis, were 0.27 (N.S.) and -0.06 (N.S.), respectively (Table 5).

Lorica and spine lengths of K. cochlearis are shown in Figure 59. During June 1975, when water temperatures were rising and numbers increasing slowly, average lorica lengths remained constant. Spine lengths, however, showed major increases in June. During late June and July, both spine and lorica lengths decreased. These decreases occurred during the warm spell in July when numbers were relatively high and stable. Both lengths remained small during August and September with some minor increases. During late September and early October, both lengths increased while the temperature dropped and the population increased slowly. A slight decline in lorica and spine lengths occurred at station C in late October. During early winter, spine lengths decreased again while lorica lengths increased. Starting in January, spine lengths increased again while lorica lengths remained stable. During early spring 1976, spine lengths increased at both stations but the increase at station C was much less than the increase at station A. Spine lengths declined during May and June while water temperatures increased. The populations showed rapid growth at both stations with station C reaching maximum numbers in mid-June. The correlation coefficient between temperature and lorica length was -0.14 (N.S.) and the coefficient between temperature and spine length was 0.49 (P < .01).

Figure 60 shows the relationship between the log of spine length and the log of lorica length. The correlation coefficient between
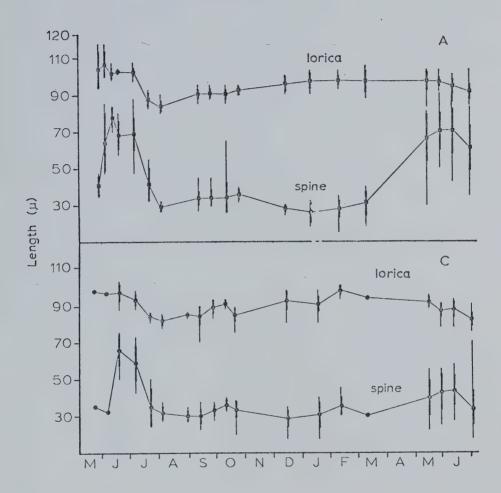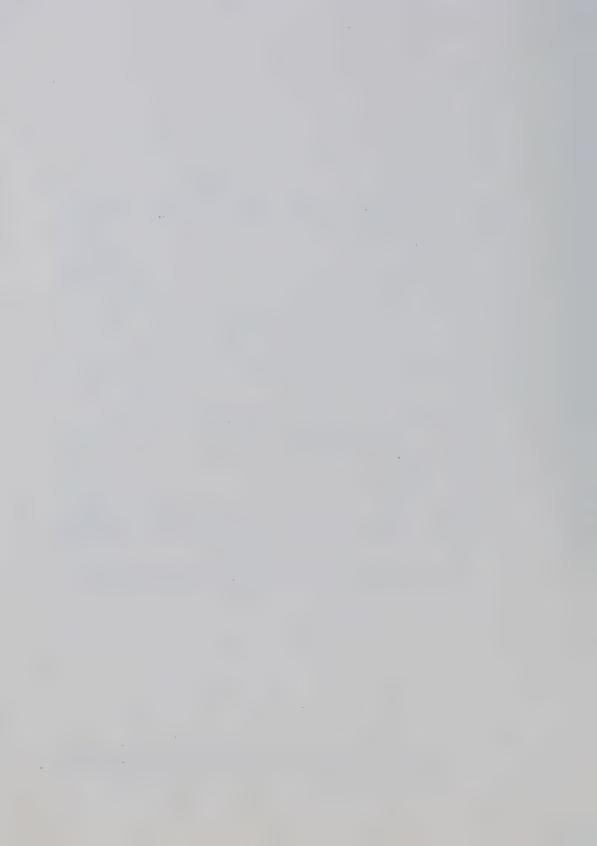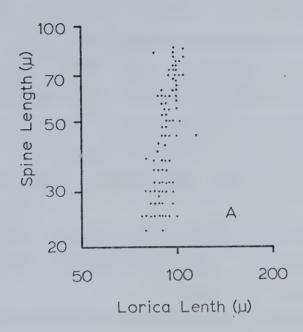
Figure 59. Average lorica and spine lengths of <u>Keratella</u> <u>cochlearis</u>
at stations A and C. 1975-1976. Thick bars indicate one
standard deviation, thin bars indicate the range.
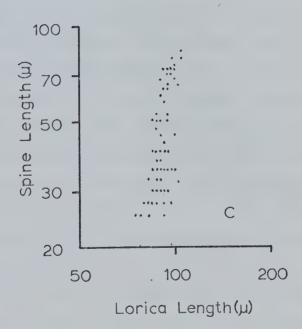
Figure 60. Relationship between lorica length and spine length of
Keratella cochlearis at stations A and C.

spine length and lorica length was 0.42 (P < .01) at station A and 0.46 (P < .01) at station C. As with the similar graph for K. quadrata, Figure 60 shows a general increase in spine length with lorica length, but there is a wide range of spine lengths for any particular lorica length. A sign test showed no significant difference between average spine lengths at stations A and C, but did show that average lorica lengths at station A were larger (P < .05) than those at station C.

Average spine lengths of K. cochlearis increased (Fig. 54) and and average lorica lengths decreased during June 1975 as the predator population grew. However, peak spine length was reached in early July while predators were still increasing and short spine and lorica lengths were associated with high predator density in August. Small increases in both spine and lorica lengths were found in fall when the predator population declined. Spine lengths dropped in winter when predators were rare, but increased in spring when predators were abundant. Lorica lengths increased slightly during winter and remained high through spring when predators were numerous. The correlation coefficient between spine length and predator density was 0.46 (N.S.) and the coefficient between lorica length and predator density was -0.47 (N.S.). Despite insignificant correlations with density of total predators, spine lengths did increase (P < .01) with an increase in density of Cyclops bicuspidatus thomasi, and lorica lengths decreased (P < .01) with an increase in density of Cyclops vernalis (Table 5).

Keratella earlinae Ahlstrom

The structure of K. earlinae is similar to K. cochlearis.
Little ecological data on this species exist in the literature, but
its feeding habits are probably similar to those of K. cochlearis.

Like K. cochlearis, K. earlinae was most common in early summer
and fall. The three populations at stations A, B, and C will be
treated separately since the population graphs (Fig. 61) show some
interesting differences. A rapid growth in numbers was seen at station
A in late May 1975. Numbers rose to a peak in mid-June, dropped
during late June, but rose again in July to a maximum on July 11.
Birth rates rose in early June, but dropped as numbers increased.
Decline in numbers during mid-June was associated with a distinct
peak in birth rate which dropped again in early July as the numbers
rose. Population density declined drastically in mid-July, but rose
again in late July and stabilized somewhat until early August when
it dropped again. Birth rates were low when the population declined
in mid-July, but rose slowly through July and were quite high when
numbers decreased in August. A small peak in numbers was seen in
mid-August, but the density decreased again during late August.
The fall increase started in early September and continued to a
maximum in early October after which the numbers stabilized. The
birth rate dropped during the mid-August peak, but started to increase
in late August. Birth rates climbed with density in early September,
but dropped quickly after the maximum density was reached in early
October. Population density remained high during December and
January. The population increase in January is somewhat surprising
considering the very low birth rate. A steady decline in numbers
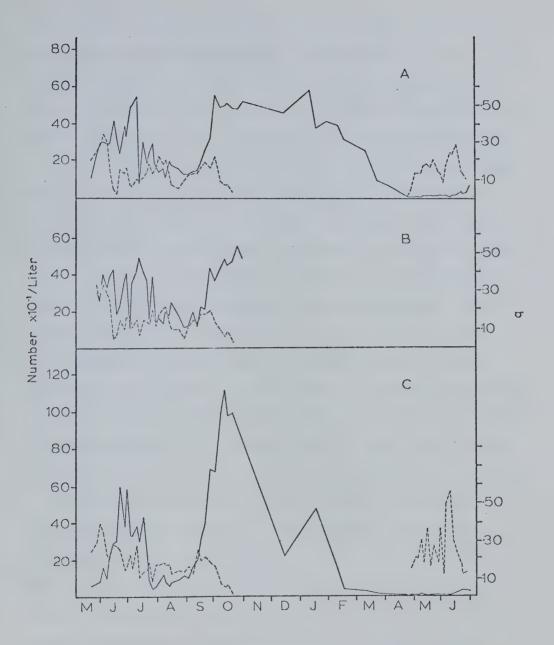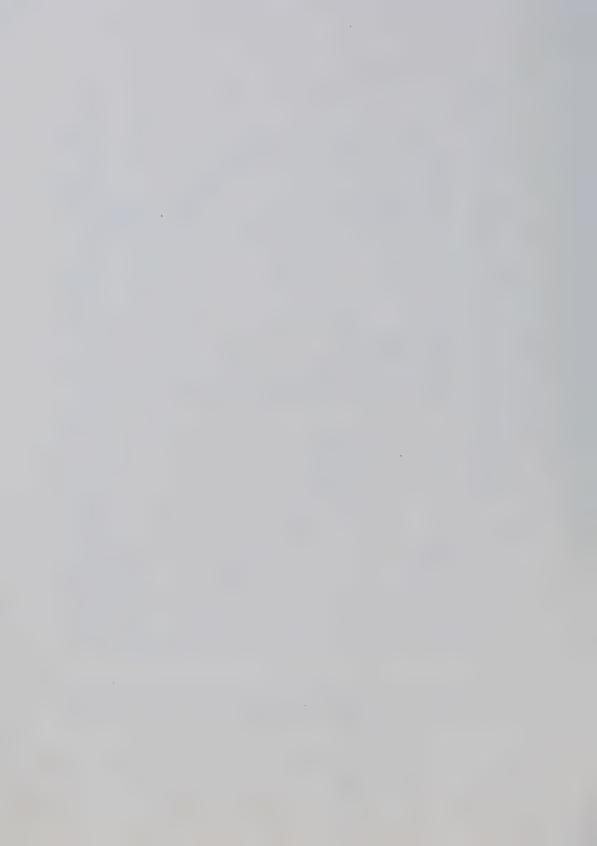
Figure 61. Population density and birth rate of Keratella earlinae at stations A, B, and C. 1975-1976.

———— density

----- birth rate

began in late January and continued until late April. During May
and June 1976, numbers remained low. A small increase was seen
in late June and early July. Birth rates were high during most of
May, but declined in early June. They rose again and were high in mid-
June but declined in late June while the population increased slightly.

Rapid population growth was not seen at station B in early spring
1975, but sampling did not start at this station until a few days
after the initial sampling at station A. Until early July, population
growth and birth rates at station B were similar to growth and birth
rates at station A. The station B population declined quickly during
early July while numbers at station A were still increasing. Birth
rates at station B were high compared with birth rates at station
A at this time. The population increased again during the second
week of July to maximum on July 14. Numbers dropped after the maximum
to a low on July 25. Birth rates declined as the maximum was reached,
but increased again when the numbers dropped. After July, population
growth and birth rates at stations A and B were similar.

The spring 1975 increase in numbers at station C appeared later
than the increase at station A. Numbers increased rapidly during
June, reaching a maximum on June 23. Numbers remained high during
late June and early July. Birth rates were high in early June, but
declined as the numbers increased. Population growth slowed around
June 20 while birth rates increased slightly. Population density
decreased in early July, but then stabilized until July 19 when a
second decline was observed. Birth rates rose after the early July
decline in numbers, but dropped immediately before the mid-July decline.
A slight pulse in birth rate occurred as numbers declined. Both

numbers and birth rates rose during late July and early August, but decreased again in mid-August. Fall population growth began slowly in mid-August; rapid growth was seen during late September and early August with numbers reaching a maximum in mid-October. Birth rates were stable during late August and early September although a small increase was noted in mid-September. In late September birth rates declined and were very low by mid-October. During early winter numbers dropped at station C. A surprising increase was seen in January but numbers dropped after this peak and population density was very low during late winter, remaining low during May and early June. Birth rates were relatively high during this time but fluctuated considerably. A very high birth rate in early June preceded a slight increase in numbers in late June. Birth rates dropped as numbers increased. The 1976 spring population at station C was similar to the population at station A but much smaller than the 1975 spring population.

When the lake water was well-mixed K. earlinae showed a uniform depth distribution (Fig. 62). In late June and early July 1975, the population concentrated in deep water which was $4 C^o$ colder than the surface water. On July 7 the majority of the population was near the bottom despite an oxygen saturation of only 11%. On July 11, oxygen concentration was less than 10% near the bottom and the population concentrated in waters directly above the area of oxygen depletion. In mid-September, the population concentrated near the bottom where the water was 40% saturated with oxygen and the temperature was $3 C^o$ less than the surface water. In December, the population concentrated near the bottom where the water was 25%
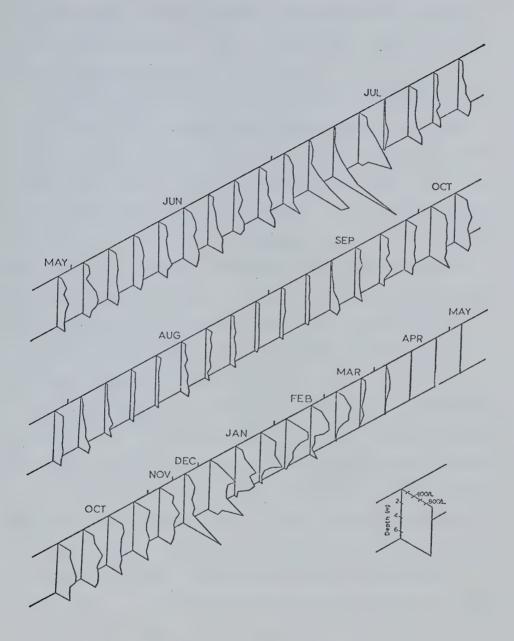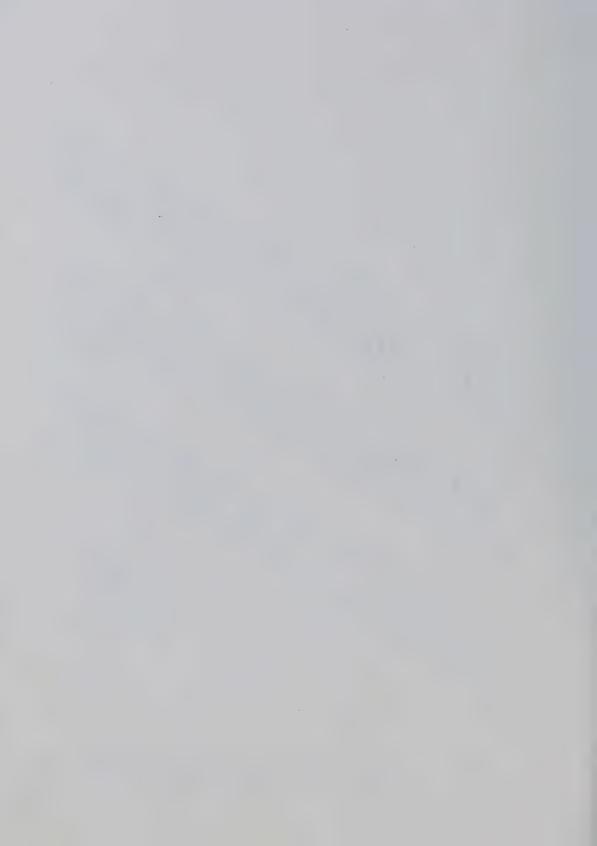
Figure 62. Vertical distribution of _Keratella earlinae_ at
station A. May 23, 1975-May 4, 1976.

saturated with oxygen. In January, the bottom three metres were less than 5% saturated and the population concentrated above the limit of 10% oxygen saturation. After ice break-up, the population was small, but appeared uniform in distribution.

Keratella earlinae was present in temperatures form 0°C to 24.5°C. Dense populations were found during the warm, calm period in July and under the ice in December. High birth rates were common in the spring, but pulses were seen in mid-summer. Birth rates were low below 10°C because of long egg duration. The vertical distribution graph (Fig. 62) indicates that K. earlinae may avoid warm temperatures when given the oppurtunity. For example, this species avoided the warm surface waters during calm periods. Ahlstrom (1943) notes that K. earlinae has been collected in North America from April to September. Horkan (1971) found specimens from 0°C to 26.6°C and noted eggs between 9.8°C and 26.6°C.

Keratella earlinae was present over a wide range of concentrations of edible cells. Population growth was seen in spring and fall 1975 when the concentration of cells was high. High birth rates occurred at times of high cell concentrations during spring and fall. However, high birth rates were also noted in summer when cell concentrations were low. The spring 1976 population showed high birth rates, but poor population growth, despite relatively high concentration of edible cells. It was also noted that the winter population at station C was lower than that at station A despite the higher edible cell concentration at station C.

The graph of birth rate and temperature (Fig. 63) shows a
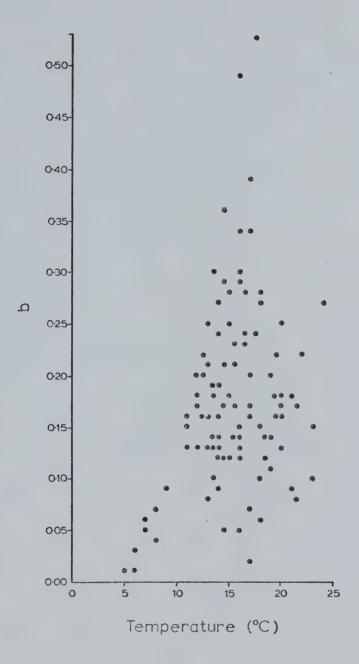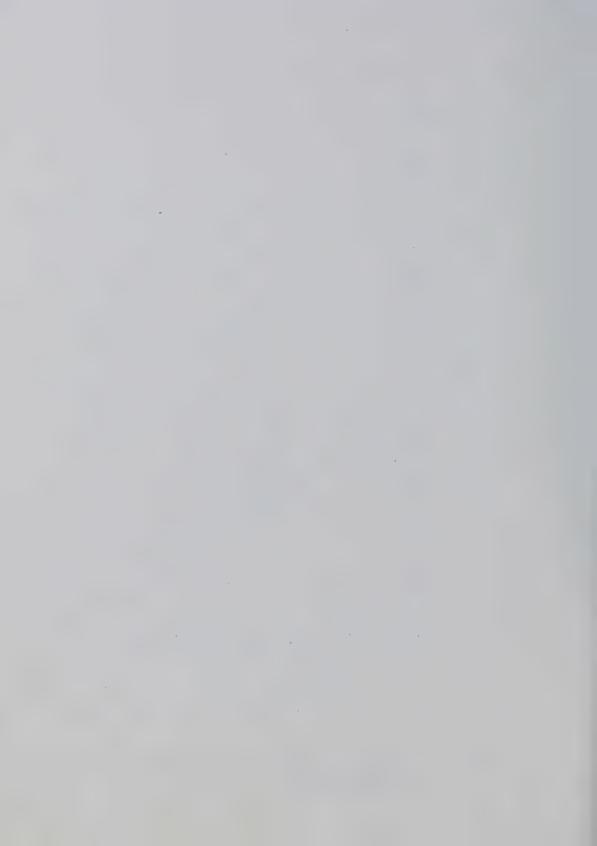
Figure 63. Relationship between temperature and birth rate of
Keratella earlinae.
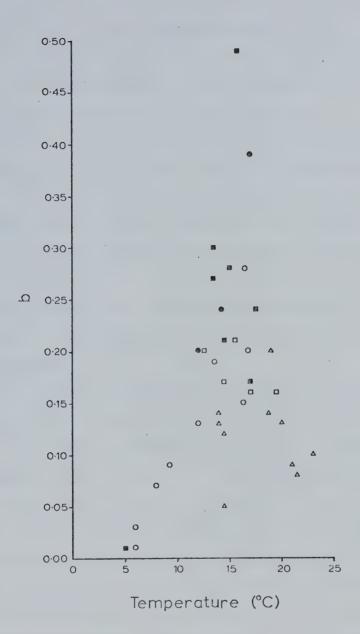
situation almost identical to that of K. cochlearis. It is noted, however, that the border appears further left in K. cochlearis than in K. earlinae. This may indicate that K. cochlearis sustains a higher birth rate at any particular temperature than K. earlinae. The correlation coefficient between birth rate and temperature is 0.57 (P < .01). The relationship between temperature, edible cell concentration and birth rate is shown in Figure 64. As expected, the border is lined with points of relatively high edible cell concentrations. Low cell concentrations are found near the bottom right hand corner of the graph. The correlation coefficient between the edible cell concentration and birth rate during the ice-free period was 0.46 (P < .01). As with the corresponding graph for K. cochlearis, some unexpected results are found. For example, at approximately 17°C a number of points of high edible cell concentrations are well below the border. The graph also shows differences from the graph for K. cochlearis. On the K. earlinae graph the black squares, indicating an edible cell concentration of 5,000-10,000/ml, are concentrated between birth rates of 0.20 to 0.25 eggs/female/day. The same points on the K. cochlearis graph are concentrated between birth rates of 0.35 to 0.40 eggs/female/day, possibly indicating that K. cochlearis can maintain a higher birth rate than K. earlinae at particular edible cell concentrations.
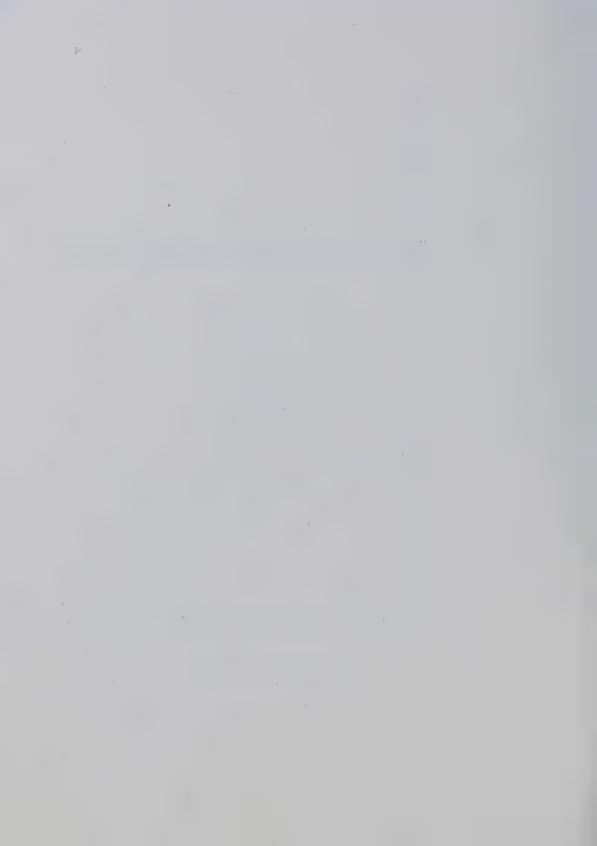
Keratella earlinae was found over a wide range of oxygen concentrations from 5% saturation to supersaturation. The vertical distribution graph shows K. earlinae moved away from areas below 10% oxygen saturation but remained in areas of only 20% saturation. In July 1975, the population concentrated in areas of 20% saturation even

Figure 64. Relationship between temperature, total edible cells, and the birth rate of <u>Keratella earlinae.</u>

     ● >10,000 cells/ml

     ■ 5,000-10,000 cells/ml

     ○ 2,500-5,000 cells/ml

     □ 1,000-2,500 cells/ml

     △ <1,000 cells/ml

though much higher oxygen concentrations were available a few metres higher in the water column. Keratella earlinae was present at station C during late winter when oxygen saturation was less than 10%. Population density at station C, however, was less than the density at station A where oxygen depletion was less severe.

Keratella earlinae was often present with K. quadrata and K. cochlearis. However, the maximum density of K. quadrata occurred earlier in spring 1975 than the K. earlinae maximum and the maximum of K. cochlearis occurred after the maximum of K. earlinae. Daphnia pulicaria populations were high during early summer 1975 when K. earlinae was dominant. The low summer populations of K. earlinae were associated with many of the other crustacean species. Small populations in early summer 1976 were associated with high densities of K. cochlearis.

Like K. quadrata, K. earlinae showed rapid population growth in late May 1975 when predators were rare. Population growth slowed in June as the predator population increased. The low densities of K. earlinae in July and August were associated with peak densities of predators. The fall increase of K. earlinae occurred as the predator population dropped. Population density of K. earlinae remained very low during May and June 1976 when Cyclops bicuspidatus thomasi were numerous. The correlation coefficient between population density of K. earlinae and density of predators was -0.65 (P < .05). The correlation coefficient between densities of K. earlinae and and C. bicuspidatus thomasi was -0.68 (P < .01) but the same relationship with C. vernalis was -0.02 (N.S.).

Average lorica and spine lengths of K. earlinae are shown in
Figure 65. The cyclomorphic pattern exhibited by K. earlinae was
almost the same, with respect to timing, as that of K. cochlearis.
During May and June 1975, spine lengths were increasing while lorica
lengths remained fairly constant. Water temperatures were rising
at this time and the population was growing. Decreases in both
lorica lengths and spine lengths were noted during July. These
decreases coincided with the warmest time of year, and with the major
population crash seen during July at station A. However, decrease
in size came before the major decrease in numbers at station C.
During August, when the water was cooling, lorica lengths appeared to
be increasing while spine lengths continued to decrease. Both
lengths increased during September while the water temperature was
dropping and numbers were increasing. During October, spine lengths
at both stations decreased while lorica lengths at station A increased
and lorica lengths at station C appeared to decrease. During early
winter, spine lengths continued to decrease while the lorica lengths
were stable. After February, spine lengths increased slowly at both
stations while lorica lengths remained stable at station A but
increased slightly at station C. In spring 1976, spine lengths increased
rapidly at both stations. Spine lengths continued to increase at
station A during June while they decreased at station C. Lorica
lengths decreased at both stations during May and June. Water
temperature was increasing during May and June 1976, but the population
was very low with a small numerical increase in late June. The
correlation coefficient between temperature and spine length was
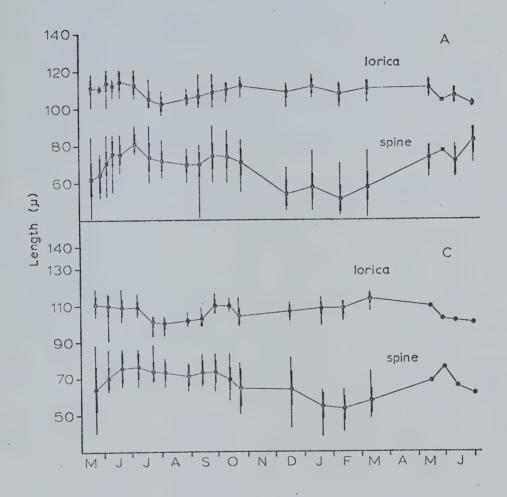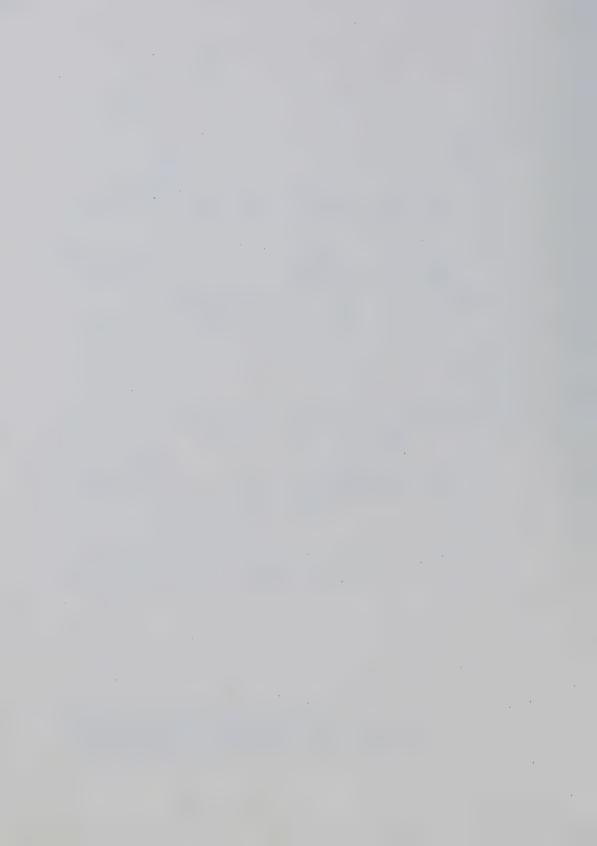
Figure 65. Average lorica and spine lengths of <u>Keratella</u> <u>earlinae</u>
at stations A and C. 1975-1976. Thick bars indicate
one standard deviation, thin bars indicate the range.
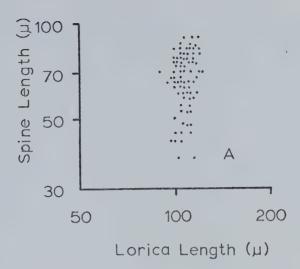
0.77 (P < .01) and the coefficient between temperature and lorica length was -0.29 (N.S.).

Figure 66 shows the relationship between spine length and lorica length for K. earlinae. The correlation coefficient was not significant at either station (0.002 at station A and -0.04 at station C). A sign test showed no significant difference between average spine lengths at station A and C, but average lorica lengths at station A were larger (P < .01) than average lorica lengths at station C.

During early summer 1975, lorica lengths of K. earlinae were stable, but average spine lengths increased with increasing numbers of predators (Fig. 54). Both lengths dropped in July when predators were still increasing and were quite short during the peak of the predator population in August. During fall 1975, spine and lorica lengths increased as predators declined. During winter, when predators were rare, spine lengths declined and lorica lengths were stable. As in 1975, spine lengths increased with increasing predator densities during spring 1976; however lorica lengths appeared to decrease. The correlation coefficient between spine length and predator density was 0.63 (P < .05) while the coefficient between lorica length and predator density was -0.74 (P < .01). Despite significant correlations between spine and lorica lengths and the density of total predators, no significant correlations were found for either length with either of the two separate predator species (Table 5).
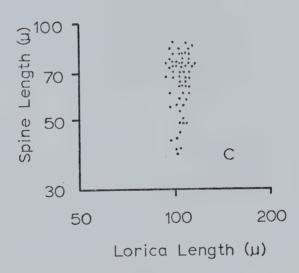
Figure 66. Relationship between lorica length and spine length of <u>Keratella</u> <u>earlinae</u> at stations A and C.

POPULATION DYNAMICS

Two basic theories can be defined concerning population regulation
(Krebs, 1972). One school maintains that factors external to popula-
tions are responsible for control, ie limiting factors, whether they
be density independent or density dependent, are the agents of
control. The other school maintains that control is mediated through
qualitative changes within a population, ie controlling factors are
evolved mechanisms which are separate from the external limiting
factors. These two points of view can be applied in connection
with studies of planktonic rotifer populations.

EXTERNAL CONTROL
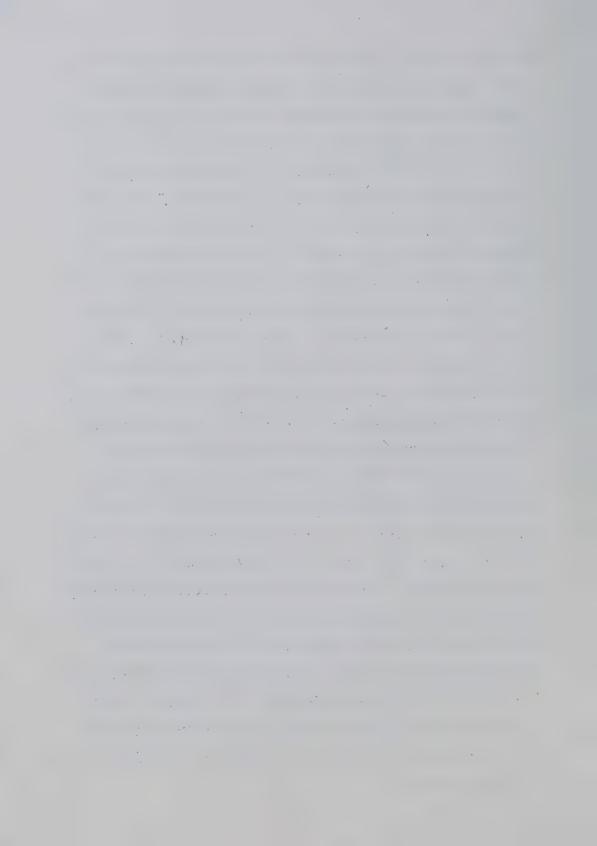
Concerning the first or "external control" theory, factors such
as temperature, food, predation, oxygen, and parasitism have been
viewed as important in controlling distribution and abundance of
rotifers (Edmondson, 1965; Pejler, 1957a,b; Ruttner-Kolisko, 1974).

Temperature

Temperature can directly affect population growth in two ways:
by acting as a limiting factor, and by altering the rate of change
of density through its effect on birth rate, death rate and length
of life. Indirectly, temperature can affect population growth by
affecting food availability, competition coefficients, degree of
parasitism, predator life history, etc. In considering temperature
as a limiting factor, Pejler (1957a) has deemed it possible to
roughly classify rotifer species according to their observed

temperature ranges. Using data from northern Swedish Lapland he defines Polyarthra dolichoptera, Keratella hiemalis and Nothalca squamula as "exclusively cold water" species, Keratella cochlearis as eurythermal, and Collotheca mutabalis as a warm water species. Ruttner-Kolisko (1974) also classified many planktonic rotifers according to their temperature limits. Results of my study often concur with such classifications but some exceptions are noted. Polyarthra dolichoptera increased in warm water despite its cold water classification and Testudinella patina was only found in warm water, despite Ruttner-Kolisko's comment, "maximum at low temperatures if at all". In my study, seasonal distribution of certain species suggests the importance of temperature as a limiting factor. Data on egg duration (Fig. 34) predict no population growth below $9^{o}C$ for Brachionus angularis and below $13^{o}C$ for Pompholyx sulcata. These predictions are born out since neither rotifer population increased below $12^{o}C$. Amren's (1964a) egg duration data for K. quadrata predicts no population growth below $1.5^{o}C$, yet increases were seen during January at $0-1^{o}C$. It is possible that the increase was due to a movement of animals into the deeper part of the lake. It is also possible, however, that the lower end of the line showing egg duration for K. quadrata in Figure 34 is not linear as shown but approaches the X axis asymptotically. If such a situation exists then the large number of eggs in November and December could have developed and caused the numerical peak in January. Decreases in birth rates of K. quadrata at temperatures above $15^{o}C$ suggest high temperatures are limiting and may explain low numbers of K. quadrata in summer.

Edmondson (1965) showed the effect of temperature on the birth rates of Keratella cochlearis, Polyarthra vulgaris, and Kellicottia longispina. He found significant correlations between temperature and birth rate for all three species, with birth rates of K. cochlearis showing the strongest relationship with temperature and Kellicottia longispina the weakest relationship of the three species. Unfortunately, Edmondson could not include data on population size in his study so, although the effect of temperature on birth rate is indicated, effects on population size can only be inferred. In my study, birth rates of K. cochlearis, K. earlinae, K. quadrata, Pompholyx sulcata, and Brachionus angularis were significantly related to temperature. However effects of birth rate on density remain unclear. High birth rates often failed to increase population density and strong population growth occurred despite relatively low birth rates.

A point that should be discussed here is effect of population age structure on birth rate. Pulses in population density of rotifers were often associated with sudden drops in birth rates. Also sudden declines in density were often associated with pulses in birth rates. When a population increases rapidly the age structure tends towards juvenile animals (Krebs, 1972). Thus when a particular rotifer population increases rapidly, the population is flooded with non-ovigerous, juvenile animals and the per capita birth rate will decrease. It is important to note that such a decrease in birth rate will occur despite stable environmental conditions; that is, a sudden drop in birth rate is not necessarily indicative of declining

environmental conditions. Pulses of birth rate occurring immediately
after a rapid decline in population density may indicate death of
a large number of senile, non-ovigerous animals and again, do not
necessarily indicate improving environmental conditions. This effect
of age structure on birth rate may explain some of the unexpected
data points shown in Figures 42, 51, 58, and 64. If a system could
be devised whereby non-ovigerous adults could be discerned from
juvenile animals, birth rates could be expressed in terms of eggs/
adult/day and would alleviate this problem.

Food

Several authors have suggested that food is important in
controlling rotifer populations (Edmondson, 1965; Pejler, 1957a;
King, 1967). However, analyses of rotifer populations pertaining to
food availability are rare due to difficulties in determining food
habits. Type and size of the mastax gives general clues as to diet,
but some reports indicate that distinct preferences are shown by
some rotifers, preferences that cannot be predicted from the feeding
apparatus. For example, Dieffenbach and Sachse (1911 in Pejler,
1957a) showed that Polyarthra euryptera will eat Cryptomonas ovata
but refuses other cells of the same size. Edmondson (1965) showed
that for three species of rotifers, certain phytoplankton species were
more important than others in affecting birth rates. Of the phyto-
plankton species studied, Chrysochromulina was the most important
in affecting birth rates of Keratella cochlearis and Kellicottia
longispina. He notes a "striking relationship between the rate of

reproduction in Polyarthra and the abundance of Cryptomonas".
Edmondson's observations on the importance of food in controlling
birth rates were supported in my study. Significant correlations
between birth rates and concentration of total edible cells were
found for Keratella quadrata, K. cochlearis, and K. earlinae. It
must be remembered that phytoplankton counts are at best a rough
estimate of food availability. Desirability of cells to zooplankton
changes according to the growth phase of cell populations (Rigler,
1971), and production of cells cannot be determined from counts.
These problems may be compounded by seasonally changing nutritional
requirements of rotifers. A certain concentration of phytoplankton
may be sufficient to sustain rotifer populations at $5^{\circ}C$ but identical
concentrations may be insufficient at $20^{\circ}C$.

By studying a laboratory population of Euchlanis dilatata,
King (1967) showed that rate of population growth was "related to
both food species and food concentration" but "ultimate density
of the population depends only on food concentration". He showed
that a diet of Chlamydomonas reinhardti maintained the highest rate
of population growth, Euglena gracilis an intermediate rate of growth,
and Euglena geniculata the lowest rate of growth. His results on
birth rate agree with Edmondson's beliefs that different food species
determine different birth rates. He found that Chlamydomonas
reinhardti maintained the highest birth rates and Euglena geniculata
the lowest birth rates, thus, control of density during the growth
phase was mediated through birth rate. King (1967) also noted that
rate of population growth was directly related to food concentration
up to a certain level, above which the population did not increase

any faster with further increases in food level. Thus, birth rate increases with food concentration until some other factor becomes limiting.

Parasitism

Ruttner-Kolisko (1974) notes that planktonic rotifers are "not infrequently" infested with parasites and that parasites may reduce "even dense populations near to extinction". Edmondson (1965) found that parasitic infestations did not affect birth rates of Keratella cochlearis, but did appear to lower birth rates of Kellicottia longispina. He noted that the importance of parasitism in K. cochlearis may have been underestimated owing to long periods between sampling dates. Unidentified parasites were seen in specimens collected from Hastings Lake, but owing to the manner of counting, it was impossible to quantify the degree of infestation. The Keratella species and Brachionus angularis were the species most often infected. Specimens of K. quadrata appeared to be particularly troubled by parasites. One live specimen of K. quadrata was so filled with a black, apparently fungal material that the mastax was pushed to one side of the body.

Predation

Few reports exist on the importance of predation on planktonic rotifer populations. Edmondson (1965) found no significant correlation between presence of the predatory rotifer Asplanchna and birth rates of K. cochlearis. This is to be expected unless Asplanchna preferentially takes either ovigerous or non-ovigerous

females. He also notes that the presence of Trichocerca capucina, which is known to attack eggs of other planktonic rotifers, made no apparent change in birth rates.

McQueen (1969), in a study on feeding rates of Cyclops bicuspidatus thomasi from Marion Lake, B.C., showed that the IV, V, and VI copepodite instars readily ate Keratella cochlearis when the rotifers were the sole prey offered. Rate of feeding increased with prey concentrations, and at a prey concentration of 700 per liter, each copepod ate approximately five rotifers per day. However, when rotifers were present along with other prey such as Diaptomus oregonensis, D. hesperus, and Cyclops nauplii, the rotifers were virtually untouched, suggesting that although rotifers can be taken, they are not preferred prey. It is difficult to fully interpret McQueen's results since no data were given concerning ratios of prey species used in mixed prey experiments, although he mentions ratios were similar to those found in the lake. Marion Lake is a small "very oligotrophic" lake (Dickman and Efford, 1972). During periods of high rainfall the lake flushes in less than 2.5 days and thus is better described as a stream than a lake (Dickman, 1969). It appears, therefore, that Marion Lake is not a typical habitat of K. cochlearis and it may be assumed that the rotifers are rare relative to other zooplankton. P. Pearlstone (personal communication) also noted low numbers of rotifers in Marion Lake. Thus low feeding rates of C. bicuspidatus thomasi on K. cochlearis in McQueen's mixed cultures may reflect this assumed paucity of rotifers. If rotifers in Marion Lake were dominant, as they were in Hastings Lake, the feeding rate may have been much higher.

Concerning the predatory behaviour of Cyclops vernalis, Fryer (1957) stated that it was "markedly carnivorous", consuming oligochaetes, copepods, chydorids, and rotifers.

Cyclops bicuspidatus thomasi and C. vernalis were the only predators studied from Hastings Lake. No predatory rotifers were found although the feeding habits of Trichocerca multicrinis may include some predation on rotifer eggs. Chaoborus were found in the lake and McGowan (1974) showed that young instars of Chaoborus anomalus and Chaoborus ceratopogones feed on rotifers in Lake George, Uganda. Unfortunately, effects of Chaoborus predation on rotifer populations could not be analyzed in my study as the plankton trap seemed ineffective in catching the agile larvae.

Table 5 shows correlation coefficients between densities of the three Keratella species and densities of the cyclopoid copepods. Keratella earlinae was the only species that appeared affected by presence of cyclopoids. The most obvious relationship is with Cyclops bicuspidatus thomasi where a strong negative correlation is found. The fact that copepodites I to III did not significantly affect density of K. earlinae supports McQueen's (1969) assumption that the older copepodite instars are the predators.

Despite insignificant correlations between predator density and density of K. quadrata and K. cochlearis, predation may still be affecting the populations. For example, in spring 1976 birth rates of both K. quadrata and K. cochlearis were high, but the population densities remained low, suggesting conditions were adequate for reproduction but some factor was reducing the number of animals.

The predator population, particularly C. bicuspidatus thomasi,
was very dense at this time and could have maintained the rotifer
populations at low densities without affecting the birth rates.

Oxygen

In any discussion of the freshwater habitat, oxygen concentration
must be included as an important environmental factor. It is
difficult, however, to determine the exact effect of various oxygen
concentrations on planktonic rotifers as the concentrations are
related to other factors, particularly temperature.

Pejler (1957a) noted that of the several species inhabiting
the hypolimnion of deep lakes in northern Swedish Lapland, only
two species, Keratella hiemalis and Filinia terminalis, could
withstand low oxygen concentrations. He also noted that Polyarthra
dolichoptera and Conochilus natans were collected from "tarns"
with a "deficiency of oxygen" in late winter when the water
temperature was low. In my study, inferences on effects of oxygen
concentration are obtained mainly from the vertical distribution
data. During the calm period in July 1975, all rotifer species
avoided areas below 10% saturation; however, several species such
as K. earlinae and Pompolyx sulcata often appeared most numerous
in waters only slightly above 10% saturation. It is doubtful
that rotifers were selecting areas of low oxygen concentration but
rather were moving to these areas to avoid some other factor,
perhaps high temperature. Thus their position in the water column
can be viewed as a balance between poor oxygen concentrations below
and high temperatures above. Concentrations of K. quadrata and

K. cochlearis near the surface during July 1975 may indicate a
greater tolerance for high temperature, although the relationship
between birth rates of K. quadrata and temperature (Fig. 50) may
indicate an inhibitive effect above 15°C. The three Keratella species
and Polyarthra dolichoptera were the only major species to exist
under the ice and P. dolichoptera was the only species to show rapid
population growth during periods of low oxygen concentration. The
Keratella species generally declined in numbers through the winter as
the oxygen concentration dropped; decline in numbers was quicker at
station C where oxygen depletion was more severe.

It is clear that external factors such as those discussed
above affect rotifer populations. However, the importance, if any,
of each factor in controlling populations remains obscure. In
discussing control, Edmondson (1965) noted that much of the literature
concerning population growth assumes a rather static reproductive
schedule and only discusses mortality as a factor in controlling
populations. It is obvious that changes in birth rate can also be
a mechanism of control. Given a set mortality rate, a population
will grow or decline depending on the difference between birth rate
and death rate. Edmondson argues, therefore, that factors such as
temperature and food availability can control population growth
through their effect on birth rate. He suggests that food avail-
ability may be a density dependent control, noting that large
populations of zooplankton can reduce food levels, thereby lowering
the birth rate.

External Control and Seasonal Abundance

In an effort to summarize effects of extrinsic factors, it is helpful to utilize the graphical models concerning aspects of control in seasonal environments proposed by Fretwell (1972). Fretwell describes a simple model in which the carrying capacity of the environment is allowed to rise and fall in a seasonal pattern and rates of population growth and decline are density independent, ie the rate of population change is positive and constant when $N < K$, negative and constant when $N > K$, and zero when $N = K$ (Fig. 67A). Despite density independent growth, perturbations in N will return to equilibrium (Fig. 67B). Fretwell complicates his model by assuming density dependence (Fig. 67C) but notes the similarity to the situation in Figure 67A.

It is apparent from Fretwell's graphs that, although the population is ultimately controlled by the carrying capacity, the density recorded at any particular time may be largely independent of it. In other words, when $K - N$ is large, N is a function of the rate of increase and the duration of that increase. As K is approached (in a density dependent system) or reached (in a density independent system) the value of N depends on the value of K.

Figures 68 and 69 are population graphs of K. cochlearis, K. earlinae, K. quadrata, Pompholyx sulcata and Brachionus angularis plotted with total edible cells, on semi-log paper, to allow comparison of the data with Fretwell's models. The graphs show obvious seasonal trends, ie K. cochlearis, K. earlinae and K. quadrata show rapid growth and large populations in spring and fall and low populations

Figure 67. Theoretical population growth in a seasonal environment.
See text for details. (Redrawn from Fretwell, 1972).

— — — density (N)
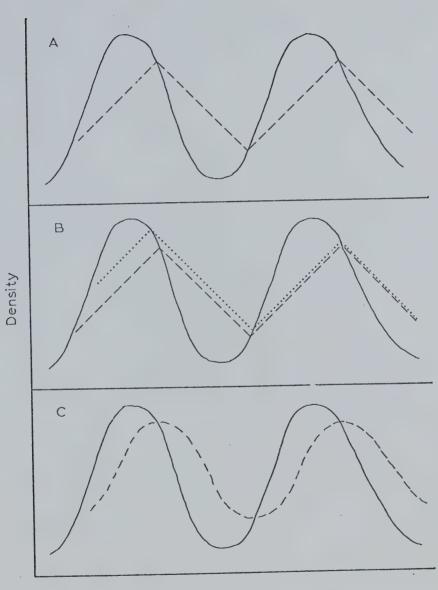
··········perturbed density

————carrying capacity (K)

A. density independent growth

B. return of perturbation to equilibrium

C. density dependent growth
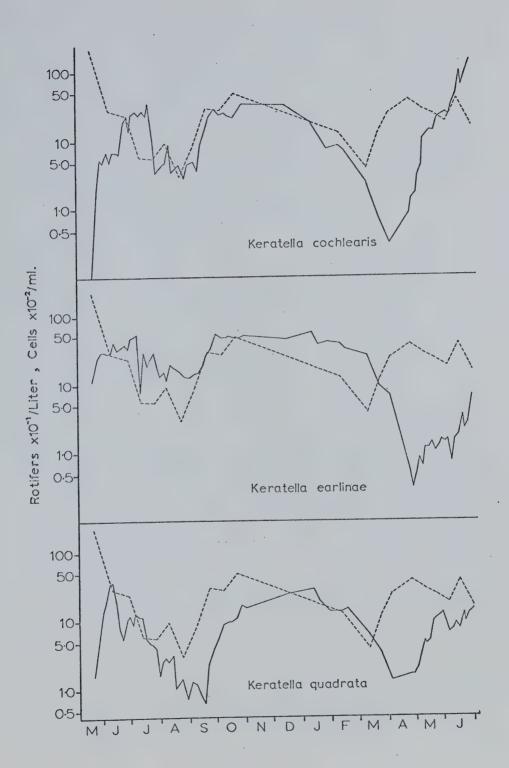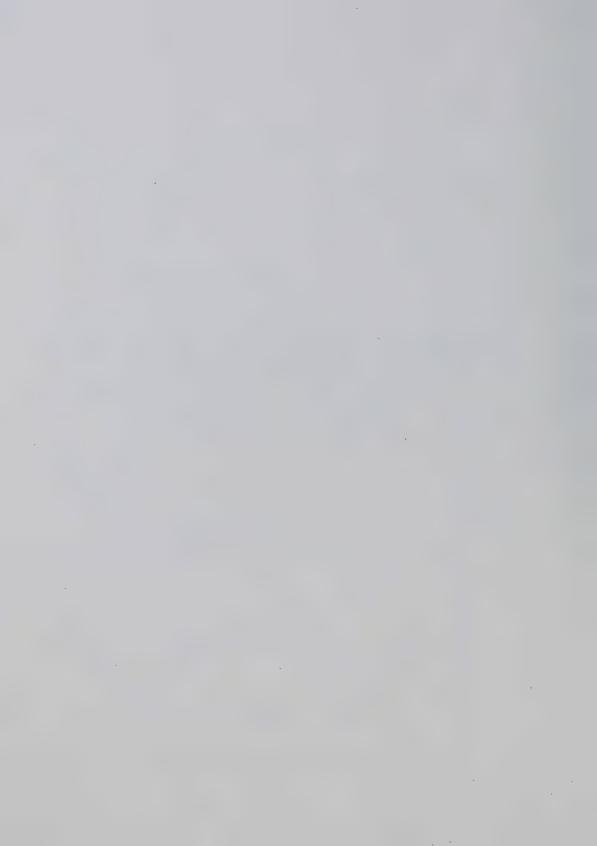
Figure 68. Logarithmic plots of the densities of Keratella quadrata, K. cochlearis, and K. earlinae with logarithmic plots of the total edible cells at station A. 1975-1976.

density of rotifers ⎯⎯⎯⎯⎯

concentration of cells ------------

Keratella cochlearis

Keratella earlinae

Keratella quadrata

Rotifers x10⁻¹/Liter , Cells x10⁻²/ml.

M J J A S O N D J F M A M J
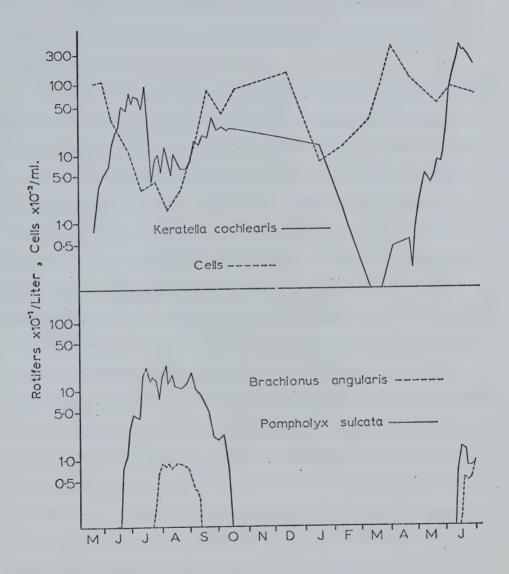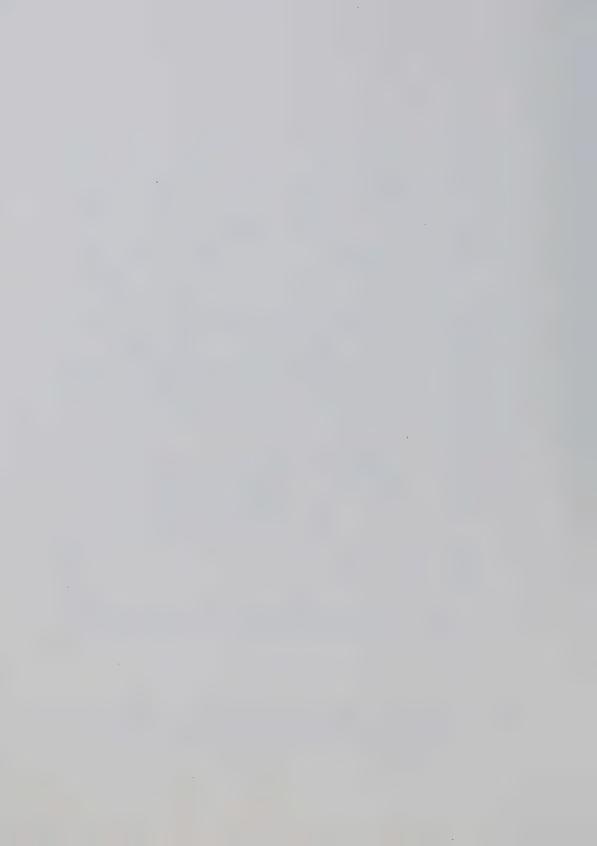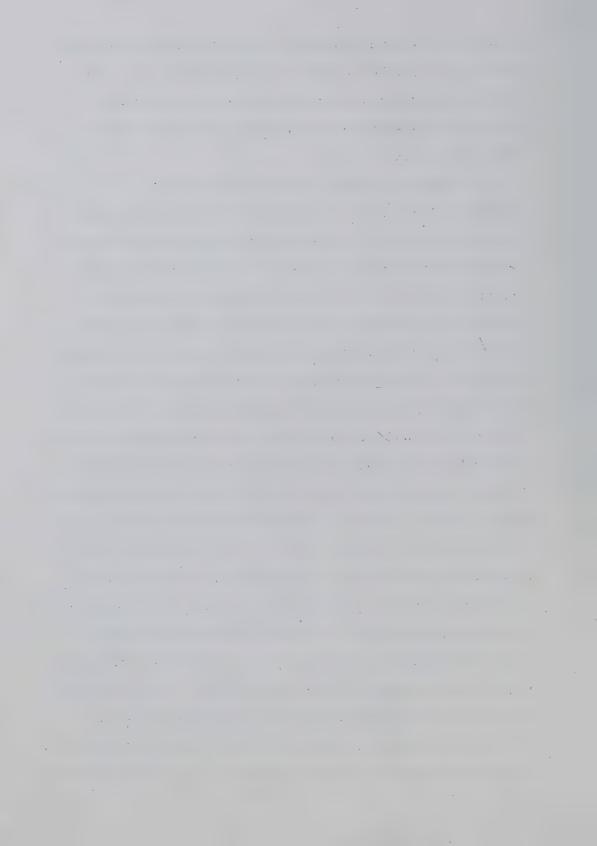
Figure 69. Logarithmic plots of the densities of Keratella cochlearis, with total edible cells, and logarithmic plots of Pompholyx sulcata and Brachionus angularis at station C. 1975-1976.

during summer, Pompholyx sulcata and Brachionus angularis show the
reverse pattern with high population densities in summer. There
are also some striking similarities between some populations,
particularly K. quadrata and K. cochlearis, and concentrations of
total edible cells.

With Fretwell's concepts in mind, and considering the environmental
factors discussed earlier, it is possible to sketch some aspects
of population growth of a perennial rotifer species in Hasting Lake.
Immediately after break-up in spring, the concentration of edible
cells is usually high but rotifer birth rates are low owing to
low water temperatures. As water temperatures rise, birth rates
increase and the population grows rapidly if there are few predators
or parasites. Such a situation was seen in spring 1975. If the
predator population is large in the spring, such as in 1976, rotifer
birth rates will be high owing to large food supplies and increasing
temperatures but population density will be low due to predation.
As spring progresses, the concentration of edible cells will decrease
owing to changes in nutrient concentrations, light levels, etc, and
perhaps zooplankton grazing. When the rotifer population reaches
the maximum density that can be maintained by the food levels it
will level off or drop. If the population levels off, it may indicate
that the carrying capacity is stable. If the population drops
quickly after reaching a maximum, it could suggest that the carrying
capacity has been reached while it is declining. This could possibly
explain the spring 1975 population of K. quadrata at station A.
The levelling off and subsequent decline in the population density
could also be caused by increased predation. Small summer populations

may be limited by low concentrations of edible cells and high densities
of predators. High _Keratella_ birth rates in summer 1975 may indicate
that food resources were sufficient for reproduction and suggest
that predators were important in maintaining low population densities.
In autumn, the concentration of edible cells will increase again
and birth rates will increase with it. If predators are rare, the
population will grow, although less quickly than the spring population
owing to colder water. Population density may level off in late
fall and early winter, possibly because it approaches the carrying
capacity but more probably because the cold water slows the reproduc-
tive rate. During early winter, population densities will remain
high as long as food supplies remain stable. Population density
will decrease during late winter because of decreases in the food
level, declining oxygen concentrations, and the increasing senility
of the population. Population curves for the _Keratella_ species
during winter suggest that rotifers live far longer than previously
expected (Ruttner-Kolisko, 1974). I believe no reproduction took
place after January yet animals were still present in April.
Numbers of animals remaining in spring are important in determining
when the spring maximum will be reached and may possibly affect the
the density at the maximum. If early spring population density is
high, the spring carrying capacity may be reached very quickly,
whereas if the early spring population is small it will take longer
to reach the carrying capacity; perhaps the rotifer populations will
not reach the carrying capacity until it starts declining. Similar
results can be expected if the early spring population is hatched

from resting eggs laid the previous fall. In this case, the number
of resting eggs produced and not the winter survival rate is important
in affecting the spring maximum.

INTERNAL CONTROL

Evidence for an "internal control" of rotifer populations comes
from work of Amren (1964a, c) and Wesenburg-Lund (1930). In his
pioneering work on life cycles of rotifers, Wesenburg-Lund classified
habitats and life histories of rotifers into several groups, paying
particular attention to the seasons and environmental conditions
under which sexual phases occurred. He studied a spectrum of habitats
from small ephemeral woodland ponds to permanent lakes. In the ponds,
he noted that the rotifer Hydatina hatched from resting eggs in spring,
reproduced asexually for a certain number of generations and
disappeared after a single sexual generation, even if the pond
remained filled for some time. He also noted that populations of
Hydatina in permanent waters also entered a resting stage after an
apparently set number of generations. He recorded that some species
of Conochiloides and Brachionus also appeared to have a set number
of generations, but noted that in certain localities some amictic
females remained after sexual periods and continued to give rise to
more amictic females. He describes the Keratella-type of life
history as maintaining amictic production all year round but capable
of producing sexual stages in any season. From such studies
Wesenburg -Lund concluded that timing of sexual periods, including
those of Keratella, is an innate mechanism that protects rotifers
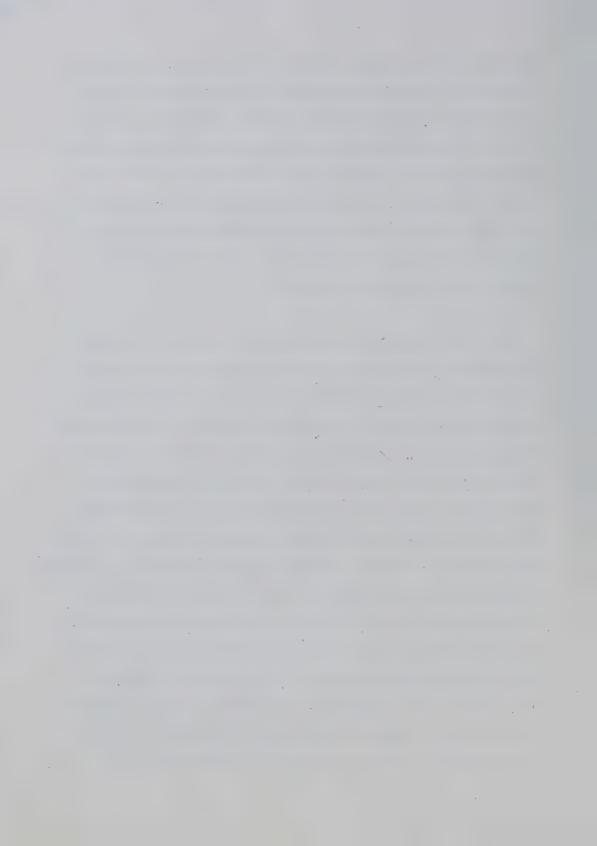
from "exceptional conditions, which ... would expose then to the greatest specific dangers". In other words the set time of sexual reproduction apparently evolved as an adaptation to ensure that the population enters a resting stage before it is decimated by rapid development of poor conditions.

Amren (1964a,c) studied populations of K. quadrata and Polyarthra dolichoptera in a pond on Spitzbergen Island. He found that birth rates of both species were not correlated with water temperature nor with concentrations of "small monads", considered to be the food source. Resting eggs of K. quadrata appeared in late July despite warm temperatures and a large population of monads. By measuring lorica and spine lengths of K. quadrata Amren was able to identify animals from the first four generations. His results show that egg ratios on any particular date were highest in the first generation, second highest in the second generation, etc. Using these data, Amren argues that decreases in birth rates seen during the study were not a result of changing environmental conditions but rather a result of differences in each generation's "internal reproductive ability". Therefore, the decrease in birth rate was due to the first generation dying out and being replaced with less productive individuals. Amren's claim that declining fertility was the major cause of lowered birth rates is debatable on a number of points. For example, his raw data indicate that certain changes in birth rates are related to temperatures. However, his recording of the decline in fertility of sequential generations seems sound and could certainly affect birth rates as he suggests, thereby acting as the

mechanism in the processes recorded by Wesenburg-Lund. In general
Amren concurs with Wesenburg-Lund's ideas concerning the adaptive
significance of limiting periods of amictic reproduction, noting
that it "may be interpreted as a sign of the rotifers having adapted
their life cycles to the most extreme conditions, ie to the years
when the drying out or ice-covering takes place unusually early".
He further states "In this way the populations avoid the risk of
drastic decimation ... and marked annual fluctuations in the
frequency are less liable to happen".

Although much is unknown concerning the importance of certain
environmental factors to rotifer populations, many of the changes
in population density in Hastings Lake can be discussed from the
view of external control. In contrast, data from this study do not
support the internal control point of view. Considering that Amren
studied small arctic ponds and that I studied a temperate lake,
the contrast in results is not surprising. If internal controls
do operate on rotifer populations as suggested by Amren, they would
most likely have evolved in distinctly ephemeral habitats. In Hastings
Lake where the seasonal changes are not as severe, a mechanism of
internal control may not be necessary. However, it can and should
be argued that an internal control could be operating in Hastings
Lake, but was not discovered due to a deficiency in methodology
for measuring such a phenomenon. Specifically, the major perennial
species were not observed to reproduce sexually, so the timing of
this period could not be compared to the favourableness of the

environment as Wesenburg-Lund could. No method for determining generations was discovered; therefore, reproductive rates of each generation could not be calculated as Amren could. The point remains, however, that while the measured environmental factors do not completely explain my results, they do indicate some control of the rotifer populations and it would appear most profitable to pursue this particular investigation by concentrating on aspects of external control.

CYCLOMORPHOSIS

Cyclomorphosis in the genus Keratella is a poorly understood
phenomenon. There are many contradictory results (Hutchinson, 1967)
that apparently stem from the inherent complexity of the material.
Lack of experimental data, and limited and often poorly designed
field studies add to the confusion. Compounding these problems
are the taxonomic difficulties with the genus Keratella. It is
essential, but often difficult, to determine whether different forms
collected over time are genetically linked and thus are exhibiting
true cyclomorphosis, or whether the forms represent different
species appearing at different times (Gallagher, 1957).

Despite such problems, a few authors have attempted to summarize
the existing data and present theories on the mechanism and adaptive
value of cyclomorphosis. Wesenburg-Lund (1900 in Pejler, 1962)
proposed that the cyclomorphic pattern displayed by planktonic
rotifers is an adaptation to maintain bouyancy. He suggested that
changes in the water's specifec gravity, caused by changes in tempera-
ture, would be sufficient to warrant a change in the bouyancy-
enhancing structures of rotifers. Ostwald (1902 in Pejler, 1962)
disputed the importance of specific gravity and suggested that
temperature-induced viscosity changes were the controlling factors.
Pejler (1962) criticized both of these ideas by noting that several
authors have found the longest spines of K. cochlearis in winter
when the specific gravity and viscosity are the greatest. He
suggested that the cyclomorphosis of rotifer spines as in K.
cochlearis, is an example of allometric growth, ie larger rotifers

develop disproportionately longer spines than do smaller forms. He suggested that low temperatures, by slowing the developmental rate, cause large forms to develop; these are forms requiring larger spines for bouyancy. Lindstrom and Pejler (1975) showed experimentally that spine lengths of K. cochlearis increase when the rotifer is cultured at low temperatures. Therefore, Pejler viewed the bouyancy of large forms as the adaptive significance of the spine variation and allometric growth as its mechanism. This begs the question; namely, what is the significance of the change in body length with temperature? Pejler (1962) referred to Margaleff (1955) on this point, Margaleff suggesting that larger animals are more efficient than smaller animals in terms of oxygen consumption at low temperatures.

In contrast to Pejler's observations of longer spines in winter, Gallagher (1957) found the spines of K. cochlearis to increase with increases in temperature during spring, and the longest spines were found at maximum water temperature, approximately 24°C. Gallagher also suggested temperature as the controlling factor in cyclomorphosis. He suggested "if the rate of growth decreases in winter and the determination of the final goal of tissues proceeds on an independent time scale, the amount of tissue for determination will be less and the structure might be smaller. In summer the reverse will be true." Gallagher did not attempt to explain the adaptive signigicance of cyclomorphosis.

Amren (1964b) studied the cyclomorphosis of K. quadrata in connection with his studies on population dynamics of rotifers

from ponds on Spitzbergen. His results show an increase in average
spine lengths during spring and summer. He provides evidence that
temporal variation is controlled by intrinsic factors, but acknow-
ledges that environmental factors may have a modifying effect.
Similar to Gallagher, Amren did not attempt an explanation of
cyclomorphosis' adaptive significance.

Data from my study do not support Pejler's (1962) theories.
The posterior spines of K. cochlearis and K. earlinae were short
during winter, longest spines being found at temperatures of 16°C
to 20°C. The correlation coefficient between spine length and
temperature was 0.49 (P < .01) for K. cochlearis and 0.77 (P < .01)
for K. earlinae; the correlation coefficients between lorica length
and temperature were -0.14 (N.S.) and -0.29 (N.S.) respectively.
Pejler's theory would have predicted a negative correlation
coefficient between temperature and spine length. I found negative
correlation coefficients for K. quadrata between temperature and
spine length and temperature and lorica length (-0.73 P < .01,
and -0.57 P < .01 respectively). This would support Pejler's theory;
however, average spine length did increase in the spring of 1976 and
data for K. quadrata, contrasting with data for K. cochlearis and K.
earlinae, would indicate that the theory cannot be applied generally.
The relationship between spine length and lorica length is also
difficult to explain by Pejler's theory. Graphs of spine length
versus lorica length for K. quadrata and K. cochlearis show a very
wide range of spine lengths for any particular lorica length,
although the general relationship is significantly positive. If
Pejler's bouyancy theory is correct, a more precise relationship

between the two lengths would have been expected. The data for
K. earlinae indicate no relationship at all between spine and lorica
length.

My data resemble Gallagher's (1957) observations; ie increasing
spine lengths in spring with maximum spine lengths in early summer
and short spine lengths in winter. Keratella quadrata, however,
possessed long spines in the winter. Pejler (1962) doubted the
importance of Gallagher's work for a number of reasons that do not
relate to my study. For example, Gallagher studied a small pond
and Pejler suggested "In such small water bodies the seasonal
variation can sometimes be the reverse of that occurring in real
lakes." However Hastings Lake is a "real" lake, and yet the pattern
of cyclomorphosis was similar to that found by Gallagher. Pejler
also noted that Gallagher's population disappeared in the winter
and appeared to be "degenerate forms that sometimes appear in small
populations." The populations of rotifers in Hastings Lake were
perennial as were those described by Pejler; but the cyclomorphic
pattern that I found was similar to the pattern shown by Gallagher's
temporal population.

Despite the similarity between the results of my study and
those of Gallagher's, it seems unlikely that Gallagher's ideas on
the mechanism of cyclomorphosis are correct. Although Pejler's
results do not compare favourably with my study or Gallagher's,
Pejler's observations of longer spines in winter is a well-documented
phenomenon, a phenomenon that Gallagher's hypothesis cannot explain.
These two workers have recorded radically different cyclomorphic
patterns, yet both have regarded temperature as the controlling
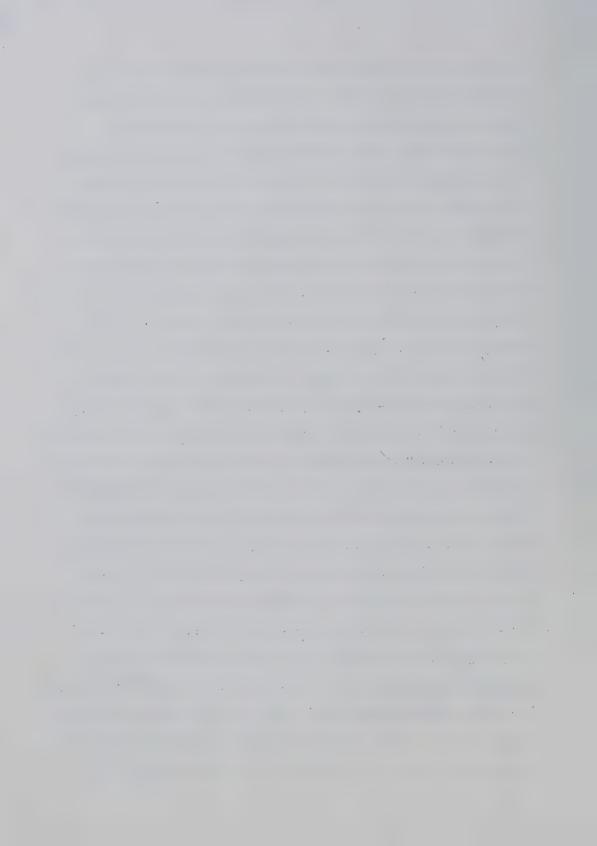
factor. Neither Pejler's nor Gallagher's hypothesis can explain one
another's data nor the data from my study, despite Pejler's (1962)
claim "It seems, after all, as though we have detected a common
denominator to all seasonal variation of zooplankters" and despite
Gallagher's (1957) claim "This work ... brings cyclomorphosis in the
Rotifera into line with that in Cladocera and Protozoa. Therefore
it now seems proper to discuss the possible underlying mechanisms
of cyclomorphosis as if it were common to all three groups."

As with data on population dynamics, it is difficult to fit
my results in with Amren's hypothesis of intrinsic control of
cyclomorphosis. An intrinsic mechanism could operate but go
unnoticed because of undeveloped methodology needed for measuring
such a phenomenon. However, in contrast to Amren's work, my data
definitely indicate that temperature is related to the cyclomorphosis
of Keratella. All three Keratella species showed significant
correlation coefficients between spine length and temperature,
although K. cochlearis and K. earlinae showed a positive relationship
and K. quadrata showed a negative relationship. The correlation
coefficient between temperature and lorica length was not significant
for both K. cochlearis and K. earlinae, but it was negative and
significant ($P < .01$) for K. quadrata. Also, the timing of the major
cyclomorphic changes in K. cochlearis and K. earlinae was similar
and apparently independent of population density, suggesting they
were both responding to the same environmental cues and were not the
result of changing age structure as suggested by Amren (1964b).

One possible factor in the cyclomorphism of Keratella, not
discussed by any of the aforementioned authors, is predation.

Several researchers working with cyclomorphic cladocerans have
suggested predation as being the ultimate cause of cyclomorphosis
(Brooks, 1965,1968; Jacobs, 1965; Green, 1967; Zaret, 1972).
Brooks (1965) noted that predation by fish is highly size selective,
(ie preferential selection of large prey), and he suggested that
the reduction in body size, observed in many planktonic cladocerans
during the summer months, is an adaptation to avoid such predation.
He noted that the large helmets produced during the period of body
size reduction are hyaline and suggested that they maintain a "critical"
biomass necessary for reproduction but are invisible to the fish,
thereby maintaining the appearance of an undesirably small food item.
However, Jacobs (1967 in Dodson, 1974) pointed out that helmets
increase the volume by only 1.1%. Dodson (1974) suggested that the
long helmets are "a response to size selective invertebrate predation",
ie the lengthening of the linear measurements is viewed as an effort
to extend body size beyond the invertebrate predators' capabilities.
Dodson's ideas and the results of my study appear contradictory.
Spine length of K. earlinae increased (P < .05) with an increase in
the numbers of total predators; however, lorica length decreased
(P < .01) and no significant relationships were found with either of
the two predator species taken separately (Table 5). Spine length
of K. cochlearis increased (P < .01) with the density of Cyclops
bicuspidatus thomasi, while lorica length did not change significantly;
but lorica length decreased (P < .01) with an increase in the Cyclops
vernalis density, while the spine length did not change significantly.
Average spine length of K. quadrata did not change significantly

with either of the two predator species, but decreased $(P < .05)$
with an increase in the total numbers of predators. Lorica length
also decreased $(P < .01)$ with an increase in the density of C. vernalis.
If changes in body size and shape are due to predation, the fact that
no significant relationships were found between rotifer measurements
and the number of copepodites stages I-III supports McQueen's (1969)
assumption that the young copepodite instars are not predacious.

Despite the poor fit of Dodson's hypothesis to my results,
predation may still act as a factor in affecting cyclomorphosis.
Strickler and Townby (1975) argued that the wake left behind a moving
zooplankter is more important in determining the behaviour of potential
predators than the actual size of the zooplankter. They described
the "prey-following" behaviour of two predaceous copepods, Epischura
nordenskioldi and Cyclops scutifer. Epischura nordenskioldi
glided smoothly through water until encountering the wake of a
potential prey. The predator then followed the direction of the
wake, being positioned slightly above it. When the predator reached
the prey, the predator dropped on it from above. Cyclops scutifer
also followed the wake of potential prey, but followed directly
down the wake and approached and captured the prey through a series
of rapid "jumps." Strickler (1975) found that C. scutifer does not
follow all the wakes it encounters. He presented photographs showing
copepods actively avoiding one another's wakes and a single copepod
avoiding a pulse of water pressure from a pipet. Copepods must,
therefore, determine whether a wake is to be followed, avoided, or
ignored. Possibly cyclomorphosis of Keratella is an adaptation to

alter the wake. Spines may function to disperse or in some way mask the normal wake, and hence reduce the probability of a predator following the wake. Unfortunately, nothing is known of zooplankton wakes, and studies on the hydrodynamics of such animals are necessary before such a hypothesis of predator avoidance can be proposed.

Another possible function of cyclomorphosis in the presence of predators is the change in the cyclomorphic animal's swimming path. Short-spined individuals of K. cochlearis rotated in a tight helix; however, long-spined K. cochlearis moved in a large open helix (Fig. 70). If the predator followed directly down the wake of a rotifer the forms with long spines may be more difficult to catch, because they would be further from the line of direction. When a rotifer was touched by a copepod (or a pipet), it immediately stopped swimming and sank passively for several seconds before resuming normal swimming behaviour. If the prey's wake is important as suggested by Strickler and Twombly (1975), this method of sinking on contact may be advantageous. For example, the rotifer would escape the area of the predator by leaving as small a wake as possible.

Gerritsen and Strickler (1977) have shown mathematically that one of the best strategies for a planktonic prey species to avoid invertebrate predation is to slow the swimming rate. This reduction in speed lowers the probability of an encounter with a predator. I found that, because of the wide sp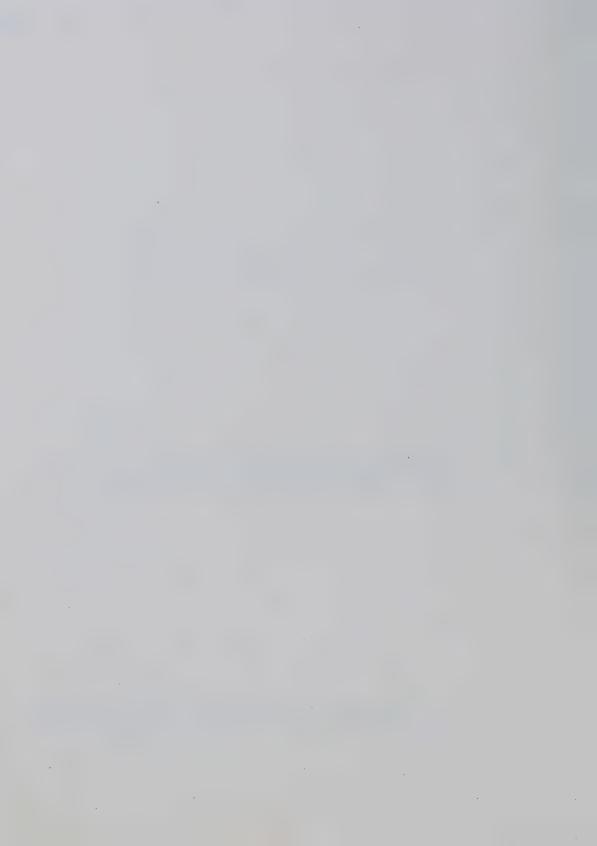iral swimming path, long-spined K. cochlearis swam slower than the short-spined forms. Hence, if spine elongation is a reaction to predation, it may function through slowing the swimming rate.

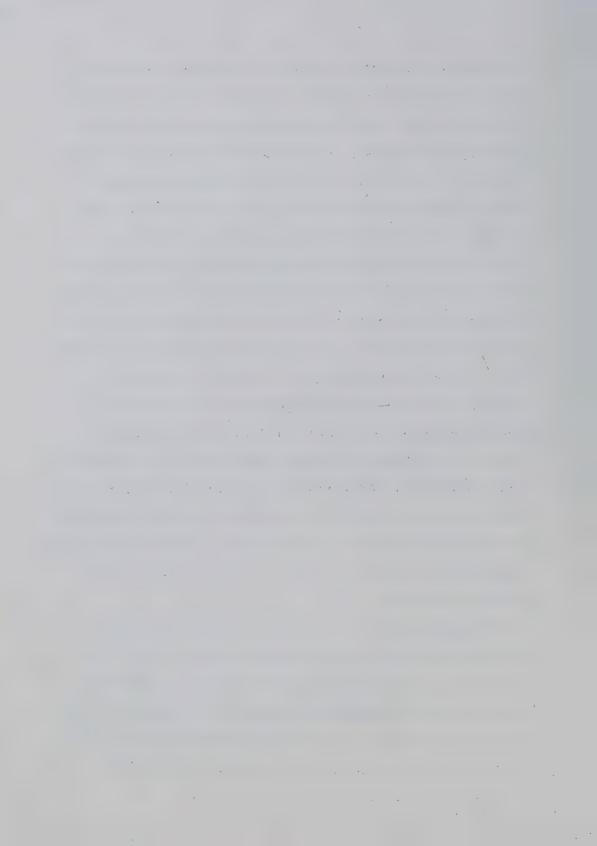If cyclomorphosis of Keratella is a reaction to predation,

Figure 70. Stylized swimming paths of long-spined _Keratella cochlearis_ (upper figure), and short-spined _Keratella cochlearis_ (lower figure).

there must be some mechanism whereby the rotifer can determine or
at least "predict" with a certain degree of accuracy, the presence
of copepods. And in this respect, temperature may be important in
affecting cyclomorphosis. If predators' life cycles are controlled
in part by temperature, as is documented for Cyclops strenuus
abyssorum (Smyly, 1973) and other Cyclops, the rotifers may react
to the predators' presence through a common temperature cue.
Hence, the relationship between temperature and cyclomorphosis may
be stronger, as in my study, than the relationship between predator
density and cyclomorphosis. If the prey responded directly to the
presence of the predator, a more sophisticated control is possible.
Such a control has been found in the relationship between the
predatory rotifer Asplanchna brightwelli and the prey rotifer
Brachionus calyciflorus (Gilbert and Waage, 1967). Asplanchna
releases a substance into the water that stimulates the precleavage
eggs of Brachionus to develop large lateral spines (Gilbert, 1967).
These spines make it difficult for Asplanchna to swallow Brachionus,
and this therefore reduces predation pressure. Perhaps cyclomorphosis
in Keratella is in some way related to chemicals released from
crustacean predators.

If Keratella species do not respond to predation pressure
through cyclomorphosis, then the observed patterns of lorica and
spine lengths and predation (Fig. 54, Table 5) may reflect a size
selective pattern of predation. For example, in Figure 54 the peaks
of predator density in summer of 1975 and spring and summer of 1976
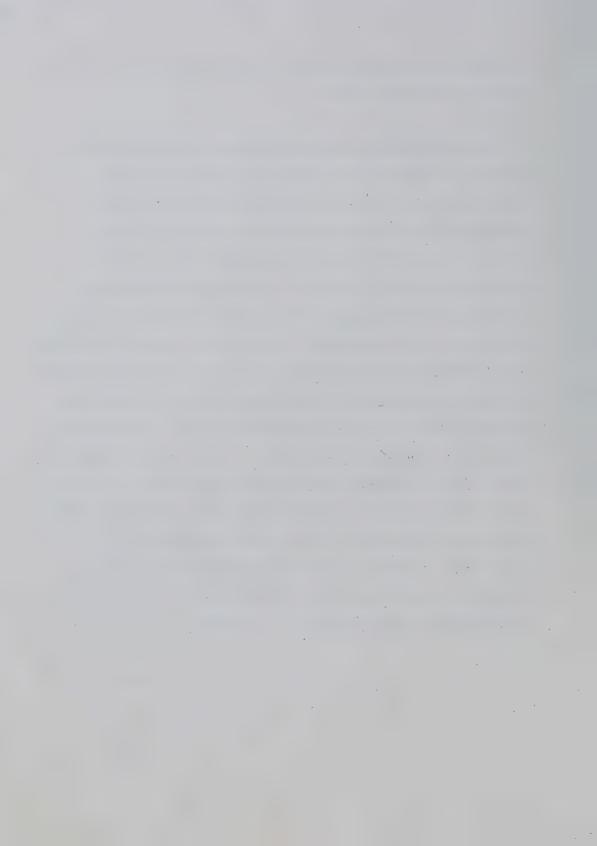were accompanied by a decrease in K. quadrata's spine length.

When predator density dropped in fall 1975, spine length rose abruptly. This may indicate that predators are selecting the largest forms, and removal of these large forms causes the average spine length to drop. However, the lower range of K. quadrata's spine lengths (Fig. 51) in July and August, 1975 is much lower than the lower range a month previously. This also holds for late spring, 1976. Although size-selective feeding may lower average spine length by reducing the upper range of values as described, it cannot extend the lower range of spine lengths. It would appear, therefore, that the decrease in spine length of K. quadrata is at least partly due to cyclomorphosis. The ranges in spine length of K. earlinae, present a problem. Keratella earlinae's spine length increased (P < .05) with an increase in the density of total predators. However, the average spine lengths and the lower range of spine lengths were lower during the peak of predator density in summer, 1975 than they were in late June when predators were less abundant (Fig. 53, 65). Thus although the general trend is for the spines of K. earlinae to increase in length with total predator density, there was a distinct decrease in spine lengths during the peak of predator density of 1975. The same conflicting pattern is seen with spine lengths of K. cochlearis. The spine length was very short during peak population density of Cyclops bicuspidatus thomasi in the summer of 1975 despite the generally positive relationship (P < .01) between spine length and density of Cyclops.

It is obvious that controlled experiments are necessary to elucidate effects of predation on cyclomorphosis. Statistical methods are useful in analyzing field data and indicating what type of
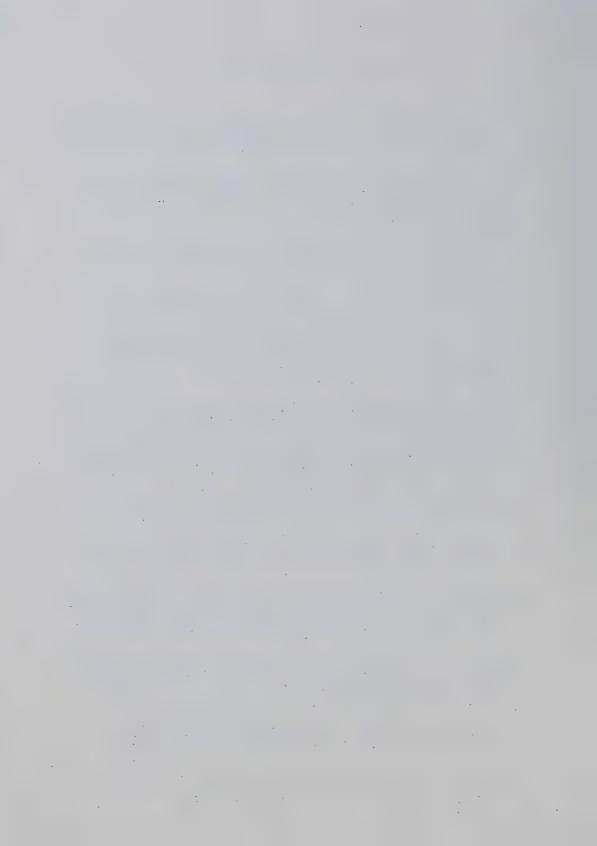
experiment would be most profitable, but are insufficient to determine cause and effect relationships.

Cyclomorphosis of freshwater animals is a fascinating subject, yet it is a difficult field, filled with numerous conflicting hypotheses. Many researchers apparently do not understand the difference between the ultimate reason for a structure and the environmental cue that triggers the development of a structure. Clearly, temperature is important in controlling cyclomorphosis, but it is now becoming apparent that temperature functions as a cue or mechanism for cyclomorphosis and is not the actual cause of cyclomorphosis. Another problem is that several researchers attempt to explain all cases of cyclomorphosis with one basic hypothesis. There is no a priori reason to assume that protozoans, rotifers, and crustaceans should change shape in the same manner. There is also no reason to assume that all species of rotifers should change shape in the same manner; indeed, there is no reason to assume that populations of the same species, living under different selective regimes, should change shape according to some species-specific format. Only by understanding the selective pressures imposed by a given environment will the causes of cyclomorphosis be discovered.

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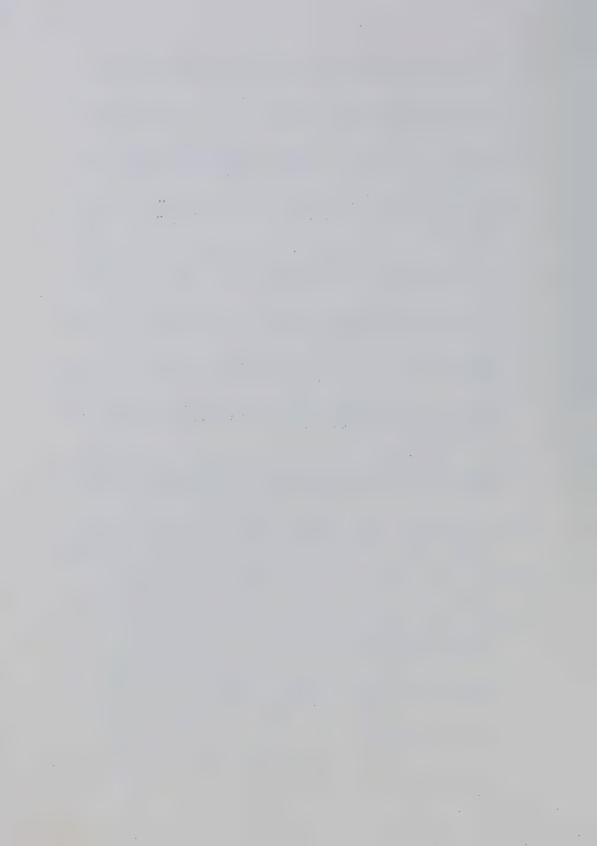Fretwell, S.D. 1972. Populations in a Seasonal Environment. Princeton University Press, Princeton. 217 p.

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APPENDIX I

Duration of development (hrs) of rotifer eggs at specific temperatures. Values expressed are minimum and maximum times of each duration.

Keratella cochlearis

Temperature

10.0°C	11.0°C	20.0°C	20.5°C
71.0-77.0	56.0-60.0	21.0-28.0	21.0-23.0
70.0-74.0		21.0-28.0	24.0-26.0
		21.0-28.0	
		24.0-27.0	
		26.0-28.0	
		22.5-24.0	

Brachionus angularis
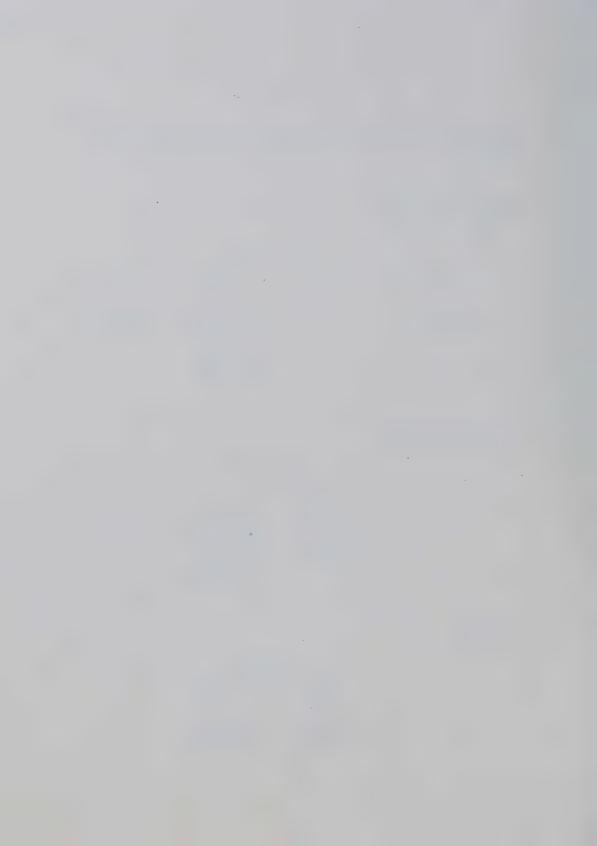
Temperature

15.0°C	19.0°C
42.0-45.5	25.0-27.0
43.0-46.0	26.0-28.5
43.0-46.0	23.5-26.5
	28.0-30.0

Pompholyx sulcata

Temperature

19.0°C	22.0°C
27.0-29.5	20.0-22.5
31.0-34.5	18.5-21.5